

COLLIGNONICERATID AMMONITES FROM THE MID-TURONIAN OF ENGLAND AND NORTHERN FRANCE

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ABSTRACT. *Collignoniceras* Breistroffer, 1947 is represented by five species in the mid-Turonian of England and Touraine (the type area of the Turonian stage) in northern France. The cosmopolitan and highly variable type species *C. woollgari* (Mantell) is shown to be a senior synonym of *C. schlueterianum* (Laube and Bruder) and *C. mexicanum* (Böse) amongst others, and shows features indicating that *Schwynoceras* Warren and Stelck, 1940 (the type species of which *S. boreale* (Warren), is also redescribed) is a synonym of *Collignoniceras* sensu stricto. Other species referred to the genus are *C. carolinum* (d'Orbigny), *C. papale* (d'Orbigny), *C. canthus* (Sornay) and *C. turoniense* (Sornay). *Ammonites fleuriausianus* d'Orbigny, 1841 is a senior synonym of *A. vielbancii* d'Orbigny, 1850 and is made the type species of *Lecointriceris* gen. nov., to which two further species, *L. carinatum* sp. nov. and *L. costatum* sp. nov. are also referred.

Collignoniceras woollgari (Mantell) is one of the most widely cited mid-Cretaceous ammonite species, giving its name to the middle zone of the Turonian standard sequence (Wright in Arkell *et al.* 1957; Rawson *et al.* 1978). As with other classic species, the type material has never been adequately figured and is of uncertain horizon, although it has at least survived the vicissitudes of a century and a half since its original description (Mantell 1822, p. 197; pl. 21, fig. 16; pl. 22, fig. 7). In England, where it was first described, the species is rare and the lectotype remains the only good adult specimen known. Elsewhere, however, it is recorded abundantly, especially in the U.S. Western Interior region, where it formed the basis of one of the early accounts of intraspecific variability in Cretaceous ammonites (Haas 1946), although as Haas and Meek before him (1876, p. 455) noted, authors have questioned whether the great majority of specimens referred to this cosmopolitan species are indeed conspecific with Mantell's types.

We have studied hundreds of European, American and Japanese *Collignoniceras* in connection with this project, and encountered an initially bewildering range of variation, both in adult ornament and the size at which ontogenetic changes occur. We have relatively few juveniles from Europe but many from the U.S.A.; conversely, large complete adults are common in European collections, but those from the U.S. are usually fragmentary. Whilst it would be possible to select individuals with differences that could be framed into diagnostic features for specific or subspecific separation, this would be misleading and conceal the over-all common features of the species recognized below. In *C. woollgari* in particular we have no doubt that a series of local races of the species existed over its wide spread, but to separate formally the successive or local populations, differing in the extent of morphological variation but overlapping, would serve no useful purpose. The broad, variable species described below not only represent reality but are adequate for detailed correlation and discussion of the evolution of the genus.

SYSTEMATIC DESCRIPTIONS

Location of specimens. The following abbreviations are used to indicate the repositories of specimens studied:

AM	Muséum de Paléontologie d'Angers.
BMNH	British Museum (Natural History), London.
CS	Château de Saumur
EMP	École des Mines, Paris (now housed at the Université Claude Bernard, Lyon).

FSM	Faculté des Sciences, Le Mans; chiefly collections formerly housed in the Musée de Tessé, Le Mans.
FSR	Institut de Géologie, Université de Rennes.
GK	Department of Geology, Kyushu University, Fukuoka.
MNHP	Muséum National d'Histoire Naturelle, Paris.
OUM	University Museum, Oxford; unless stated otherwise, these are collections made by Hancock and Kennedy.
SP	Collections of the Sorbonne, now Université de Paris VI.
WW	C. W. and E. V. Wright collection.

Dimensions. All dimensions are given in millimetres; figures in parentheses are the dimensions as a percentage of the total diameter. D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; Ic = intercostal; c = costal; R = number of ribs per whorl.

Suture terminology. The suture terminology of Wedekind (1916; see Kullman and Wiedmann 1970 for a recent review) is followed here: I = Internal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

Suborder AMMONITINA Hyatt, 1889

Superfamily ACANTHOCERATACEAE de Grossouvre, 1894

[*nom transl. et correct.* Hyatt 1900, *ex* Acanthoceratidés de Grossouvre, 1894]

Family COLLIGNONICERATIDAE Wright and Wright, 1951

Subfamily COLLIGNONICERATINAE Wright and Wright, 1951

Genus COLLIGNONICERAS Breistroffer, 1947

(*non* Van Hoepen, 1955)

Type species. *Ammonites woollgari* Mantell, 1822 by the original designation of Meek (1876) as type species of *Prionotropis* Meek, 1876 (*non* Fieber, 1853), for which Breistroffer (1947) proposed *Collignoniceras* as *nomen novum*.

Diagnosis. Medium to large, moderately involute to evolute ammonites. Early whorls compressed, parallel sided, ornamented by crowded or sparse, prorsiradiate, straight or flexuous ribs, mostly long, with weak to strong umbilical bullae. All ribs bear in the early stages outer ventrolateral tubercles in addition to siphonal clavi.

This style of ornament is, in some species, retained to maturity. In most, however, the ribs coarsen, become widely spaced, with strong to weak umbilical tubercles (which migrate progressively outwards from the umbilical margin), prominent inner and outer ventrolateral tubercles which may fuse into a massive horn or flared rib, from which commonly arise pairs of low ribs, joining siphonal clavi more numerous than the ventrolateral and linked into a more or less continuous keel. Rarely the ornament is greatly reduced on the body whorl.

The sutures are little incised, with massive saddles.

Discussion. The diagnosis given above summarizes the rather wide variation seen in species referred to this genus, which include *C. boreale* (Warren), *C. papale* (d'Orbigny), *C. canthus* (Sornay), *C. turoniense* (Sornay) and *C. carolinum* (d'Orbigny). The nomenclatorial history of the genus is somewhat complex. Meek introduced a subgenus *Prionotropis* in 1876, with *Ammonites woollgari* Mantell as type species. Breistroffer (1947) pointed out the prior usage of *Prionotropis* by Fieber (1853) and proposed *Collignoniceras* as *nomen novum*. Meanwhile Warren and Stelck (1940) had proposed the genus *Selwynoceras* with *P. borealis* Warren, 1930 as type species, distinguishing it from Meek's *Prionotropis* by the presence of a row of nodes instead of a keel on the inner whorls and the marked alternation in length and strength of the ribs. Wright (in Arkell *et al.* 1957, p. L426) regarded *Selwynoceras* as a subgenus of *Collignoniceras*, whilst Powell (1963, p. 1223) considered the two synonymous. Following an application by Matsumoto and Wright in 1966, the International Commission on Zoological Nomenclature ruled in 1968 (Opinion 861) that *Collignoniceras* Breistroffer, 1947, should be given priority over *Selwynoceras* Warren and Stelck, 1940, by those who regard the two as synonyms.

From a comparison of the types and other specimens of *C. woollgari* and *S. boreale*, we would agree with Powell that the two do not bear even subgeneric separation: *boreale* is simply a small species of *Collignonicer* in which the flared ribs appear at a relatively early stage. The ventral tuberculation visible on the outer whorl of the lectotype (here designated), which is refigured here as Pl. 70, figs. 1–2, is on exactly the same plan as in English *woollgari*, whilst, as Haas (1946), Powell (1963) and Matsumoto (1965) have shown, the style of ribbing of juvenile *Collignonicer* is very variable.

Collignonicer differs from *Prionocyclus* Meek, 1876 (type species *P. wyomingensis* Meek) in that the latter has very fine dense irregular ribs through most or all of its ontogeny and a broader venter with an entire or serrated keel. *C. woollgari* and *P. hyatti* (Stanton) overlap in time in the southern U.S. and some late *C. woollgari* there and also in Europe show a low siphonal keel at maturity, emphasizing the intimate relationship between the two. Ribbing is usually dominant over tuberculation in *Prionocyclus*, although some species bear finger-like ventrolateral spines, foreshadowing the development seen in the later *Prionocycloceras* (Young 1963, pl. 23, figs. 1–6; pl. 27, figs. 2–4). Matsumoto (1965, p. 19) discusses other differences between these two genera.

Subprionocyclus Shimizu, 1932 was originally separated from *Collignonicer* [*Prionotropis*] on the basis of minor differences between the internal sutures. As Matsumoto (1959, p. 109) notes, however, distinguishing features also include the paired or alternately long and short sigmoidal ribs of *Subprionocyclus* which may flatten on the outer whorl, greater persistence of outer ventrolateral tubercles and absence of massive horns. Like *Prionocyclus*, *Subprionocyclus* has a continuous persistent keel which varies with the density of the ribbing from finely to coarsely serrate.

Germanicer Breistroffer, 1947 is perhaps only doubtfully separable from *Prionocyclus*; known only from juveniles, it may be separated from *Collignonicer* by the possession of fine dense narrow ribs with small sharp umbilical, inner and outer ventrolateral tubercles and a finely serrated continuous keel with more serrations than the number of ventrolateral tubercles.

Reesidites Wright and Matsumoto, 1964, which should perhaps be placed in Barroisiceratinae, is compressed and involute, high whorled, with a fastigiate venter; sinuous ribs branch in groups of two or three from small umbilical bullae, with single ventrolateral and siphonal clavi only. The largest individuals barely exceed 100 mm diameter (Matsumoto 1965).

Subprionotropis Basse, 1950, known only from specimens a few centimetres in diameter, differs from *Collignonicer* in being involute with compressed whorls, with ribs arising in pairs from umbilical bullae (with additional intercalated ribs) bearing only ventrolateral and siphonal clavi and forming strong chevrons on the fastigiate venter. At the end of the body chamber, ribs and tubercles weaken and the venter becomes rounded.

Lymanicer Matsumoto, 1965 and *Niceforoceras* Basse, 1948 are both compressed and involute, with weak, dense flexuous ribs or striae, a single ventrolateral tubercle and a finely serrated keel.

Collignonicer is the earliest genus of Collignoniceratidae to appear in the Turonian, and, as Matsumoto (1965) has noted, some individuals in variable United States Western Interior populations show early whorls which foreshadow *Prionocyclus*, *Subprionocyclus* and thence the remaining late members of the group.

With respect to the evolutionary origins of the genus, Wright (in Arkell *et al.* 1957, p. L426) and Matsumoto (1965, p. 10) have suggested that the diminutive late Cenomanian acanthoceratid *Protacanthoceras* Spath, 1923 might be the ultimate ancestor, with *Neocardioceras* Spath, 1926 as an intermediate. Recent collecting from the latest Cenomanian/early Turonian faunas of the condensed *Neocardioceras* Pebble Bed of Devon (see Hancock, Kennedy and Wright 1977, fig. 2 for details) has now produced a range of specimens that provisionally we refer to *Thomelites* Wright and Kennedy, 1973, among which are individuals with siphonal clavi tending to form a continuous serrated keel. In addition, a few poorly preserved fragments seem already to have reached the stage of *Collignonicer* in some features of decoration. There remains, however, a gap in the European successions, corresponding to most of the *Mammites nodosoides* assemblage Zone, in which the genus is absent apart from a single possible example in the collection of Colonel O. H. Bayliss, from Shapwick, Devon; W. A. Cobban (*in litt.*, 1978) tells us that *Collignonicer* appears at the top of the North American correlatives of this zone.

Occurrence. *Collignoniceras* is widespread in the middle of the Turonian stage, the classic *woollgari* Zone. There are records from England, France, Germany, Czechoslovakia, Poland, Rumania, Turkestan, Japan, California, Texas, the U.S. and Canadian Interiors, Greenland, north Africa, Colombia, and northern Australia.

Collignoniceras woollgari (Mantell)

Plates 62–67; Plate 69, figs. 3–4; Plate 71, figs. 1–3; text-figs. 1A, 2–4

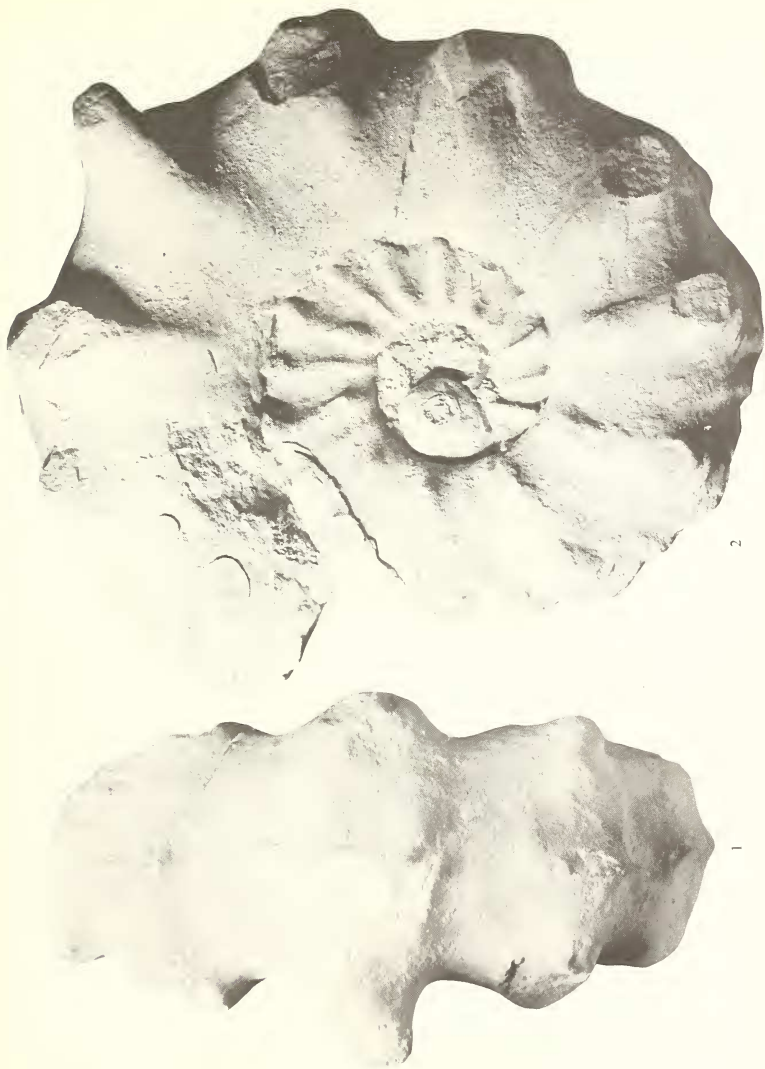
- 1822 *Ammonites Woollgari* Mantell, p. 197, pl. 21, fig. 16; pl. 22, fig. 7.
 non 1841 *Ammonites Woollgari* Mantell; d'Orbigny, p. 352, pl. 108, figs. 1–3.
 1850 *Ammonites Woollgarii* d'Orbigny, p. 189 (*pars*).
 1855 *Ammonites Woollgari* Mantell; Sharpe, p. 27, pl. 11, figs. 1, 2.
 1860 *Ammonites carolinus* (d'Orbigny); Courtiller, p. 251, pl. 3, fig. 2.
 1867 *Ammonites Woollgarii* Mantell; Courtiller, p. 7, pl. 8, figs. 1–4.
 1872 *Ammonites Woollgari* Mantell; Schlüter, p. 25, pl. 9, figs. 1–5; *non* pl. 12, figs. 5, 6.
 1872 *Ammonites Woollgari* Mantell; Geinitz, p. 184, pl. 33, figs. 1, 2 (?), *non* 4–5.
 1872 *Ammonites Woollgari* Fritsch, p. 30 (*pars*), pl. 3, figs. 1–3; pl. 4, figs. 1–2; pl. 14, fig. 6; *non* pl. 2, figs. 1–2; pl. 15, fig. 6.
 1887 *Acanthoceras Woollgari* (Mantell); Laube and Bruder, p. 235, text-fig.
 1887 *Acanthoceras Schlüterianum* Laube and Bruder, p. 236, pl. 29, figs. 2–3.
 1902 *Acanthoceras Woollgari* (Mantell); Petrascheck, p. 149, text-figs. 7–8.
 1902 *Acanthoceras* *cf.* *Woollgari* (Mantell); Petrascheck, p. 148, pl. 12, figs. 2–3.
 1902 *Acanthoceras Schlüterianum* Laube and Bruder; Petrascheck, p. 150, pl. 10, fig. 3; pl. 11, fig. 3; pl. 12, fig. 1.
 1907 *Prionotropis Schlüterianum* Laube and Bruder; Pervinquier, p. 275.
 1925 *Prionotropis Schlüteriana* Laube and Bruder; Diener, p. 156.
 1928 *Prionotropis woollgari* Mantell var. *mexicana* Böse, p. 262, pl. 11, figs. 11, 12.
 1931 *Pseudaspidoceras* (?) *chispaense* Adkins, p. 51, pl. 3, figs. 1–2.
 1931 *Pseudaspidoceras* ? sp. Adkins, p. 53, pl. 2, fig. 2.
 1931 *Pseudaspidoceras* (?) n.sp. A; Adkins, p. 53, pl. 3, figs. 3–4.
 1946 *Prionotropis woollgari* Meek (? *non* Mantell); Haas, p. 150, pls. 11, 12; pl. 13, figs. 1–3, 5–18; pl. 14, figs. 1–10, 12–16; pl. 15, figs. 1–6, 9, 10; pls. 16, 17; pl. 18, figs. 1–2, 7–9; text-figs. 1–91.
 1963 *Selwynoceras mexicanum* (Böse); Powell, p. 1225, pl. 166, figs. 2–7; pl. 167, figs. 1, 3–8; pl. 168, fig. 4; text-figs. 2–4.
 1971 *Collignoniceras woollgari* (Mantell); Matsumoto, p. 130, pl. 21, fig. 4, text-fig. 1.
 1972 *Collignoniceras woollgari* (Mantell); Cobban and Scott, p. 94, pl. 14, fig. 5; pl. 30, fig. 1; pl. 37, figs. 9–10 (with additional synonymy).
 1975 *Collignoniceras woollgari* (Mantell); Hattin, pl. 10, figs. N, P, Q, R.
 1977 *Collignoniceras* (*Selwynoceras*) *schlueterianum* (Laube and Bruder); Hancock, Kennedy and Wright, p. 156.
 1977 *Collignoniceras* (*Collignoniceras*) *cf.* *C. woollgari sensu* Matsumoto, 1965, group E; Hancock, Kennedy and Wright, p. 156.

Types. The lectotype, designated by Wright and Wright (1951, p. 35), is BMNH 5682, from the Middle Chalk of Lewes, Sussex, refigured here as Plate 62, figs. 1–2; Plate 63, fig. 9. Two additional specimens from Mantell's collection, BMNH C5742 a–b (Plate 69, figs. 3, 4), are presumed to be paralectotypes.

Other specimens studied. These include: BMNH 4863 a–b, from the Middle Chalk 'near Lewes, Sussex'; BMNH 43963 'Lower Chalk, near Lewes' (J. de C. Sowerby Collection); BMNH C30394 'Turonian Mount Caburn Pit, near Glynde, Sussex' (labelled aff. *woollgari* by L. F. Spath); BMNH C40152 from the Middle Chalk, *Terebratulina lata* Zone, Mickleham Bypass, Surrey (C. W. and E. V. Wright Collection); WW 16682, 14792–4, from the Middle Chalk, top of the *T. lata* Zone Middle Chalk, Mickleham Bypass, Surrey; WW 22925–7, Middle

EXPLANATION OF PLATE 62

Figs. 1–2. *Collignoniceras woollgari* (Mantell). The lectotype, BMNH 5682, from the Middle Chalk of Lewes, Sussex.



KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

Chalk, Lewknor Crossroads, Lewknor, Oxon. (ex R. E. H. Reid Collection); OUM K 10273, K 10275-76 from no more than 5 m below the top of the Chalk Rock at Fognam Barn, Berkshire, 3 km WNW of Lambourn. BMNH 88988 b, 88989 a-c from the Turonian of the White Mountain, near Prague, Czechoslovakia.

French specimens include the following: OUM KZ 741, 743-4, 746, 748-9, 753, from the St. Cyr-en-Bourg Fossil Bed, Champignonnière Les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay, Maine-et-Loire, and numerous specimens in the Muséum de Paléontologie, Angers, from this bed and adjacent levels in the Tuffeau Blanc (Couffon Collection etc.) variously labelled Saumoussay, St. Cyr-en-Bourg, Saumur, and elsewhere, including AM 57, AM 59, AM 116.

There are numerous specimens from Poncé, Sarthe, and others from Bourré in the Cher Valley, Loir-et-Cher, including BMNH C74803.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>	<i>Ribs</i>
Lectotype	130 (100)	40 (31)	40 (31)	1	50 (38)	13
FSR, C273	67.3 (100)	20.4 (30)	25.0 (37)	0.81	23.9 (36)	24
MNHP W7	58.5 (100)	21.0 (36)	— (—)	—	22.8 (39)	19
MNHP W18	61.0 (100)	24.0 (39)	23.7 (39)	1.01	22.0 (36)	22
MNHP 'X'	86.0 (100)	29.0 (34)	34.9 (41)	0.83	29.5 (34)	~20
MNHP W15	81.0 (100)	32.0 (40)	32.0 (40)	1.0	27.8 (34)	19
MNHP lc	141.0 (100)	52.0 (37)	49.5 (35)	1.05	55 (39)	—
lc		41.5 (29)	49.5 (35)	0.83		
MNHP 6778	133.0 (100)	45.0 (34)	50.0 (38)	0.9	44.5 (33)	18
MNHP W20						
lc	162.0 (100)	55.0 (34)	52.0 (32)	1.05	67 (41)	—
MNHP W4 c	137.0 (100)	60.0 (43)	51.0 (37)	1.18	— (—)	15/16
lc		39.5 (29)	39.5 (29)	1.0		
MNHP W10	109.0 (100)	47.5 (44)	42.0 (39)	1.13	37.0 (34)	—
		33.5 (31)	38.8 (36)	0.86		
MNHP W19	175.0 (100)	74.8 (43)	65.0 (37)	1.15	65.0 (37)	15

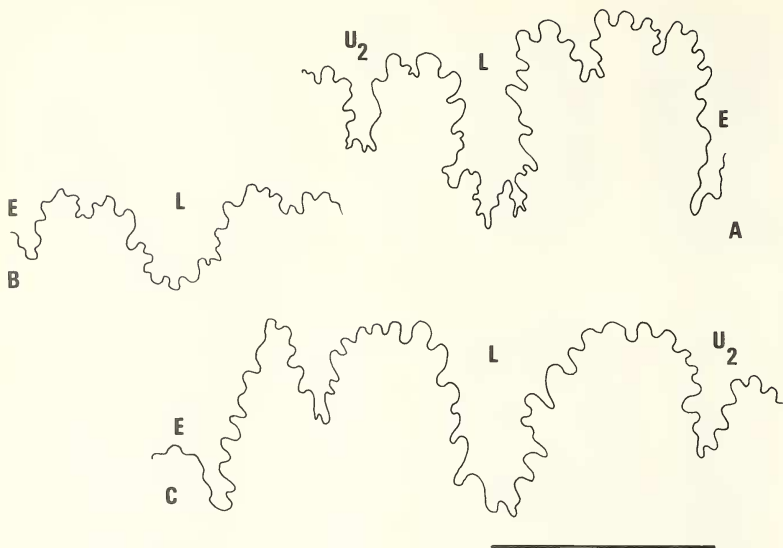
Description. The inner whorls of our smallest specimens show coiling to have been moderately evolute, with compressed whorls and a shallow umbilicus. At about 10–15 mm diameter, there are 27–32 ribs per whorl; the density decreases with increasing size. The ribs are even, bar-like, prorsiradiate, straight and clearly demarcated from the flat interspaces. As size increases, ribs become much more widely spaced; at 40–50 mm diameter there are only 17–24 ribs per whorl. They are of variable strength, arise from weak to strong umbilical bullae and are narrow, high and separated by wide, flat interspaces; they are markedly prorsiradiate and straight to concave on the flanks, always single, with no intercalated ribs. At the ventrolateral shoulder they bear conical to feebly clavate inner ventrolateral tubercles. From these the ribs are either weakly or strongly projected forwards to elongate outer ventrolateral clavi. A broadened swelling connects these in turn to a sharp, continuous siphonal keel, strengthened into sharp high clavi at the peak of the variably angled ventral chevron formed by the termination of the ribs.

This type of ornament may extend to diameters of 100 mm, but typically, as size increases, a series of changes in ornament occur, more or less independently of each other. The umbilical bullae move outwards and come to occupy a lower flank position, whilst the ribs are differentiated into long bullate ones and (in most specimens) from one to four shorter ribs, restricted to the outer flank and venter and sometimes lacking ventrolateral tubercles. The inner ventrolateral tubercles may at this stage develop into a distinctive conical horn which supports, on the outer flank of its base, the outer ventrolateral clavus; some specimens present a ventral aspect in

EXPLANATION OF PLATE 63

Figs. 1–12. *Collignoniceris woollgari* (Mantell). 1–4, OUM KZ 746; 11–12, OUM KZ 748, from the St. Cyr-en-Bourg Fossil Bed, Champignonnière Les Rochains, south of Saumur and north-east of Montreuil-Bellay, Maine-et-Loire. 5–6, MNHP 6778 (d'Orbigny Collection), Poncé, Sarthe; 7–8, OUM KT 1160, from the Ojinaga Formation at Cannonball Hill, northern Chihuahua, Mexico. 9, Apertural view of the lectotype, BMNH 5682; see explanation of Plate 62 for details. 10, MNHP W1, 'Le Mans, Sarthe' (from Poncé?). Figures 1–2 are $\times 2$; the remainder are $\times 1$.





TEXT-FIG. 1. Sutures of *Collignoniceras* species. A, *C. woollgari* (Mantell), from BMNH C74803; B, *C. carolinum* (d'Orbigny), from the Sorbonne specimen (de Grossouvre Collection); C, *C. papale* (d'Orbigny), from a Sorbonne specimen (de Grossouvre Collection). Bar scale is 2 cm.

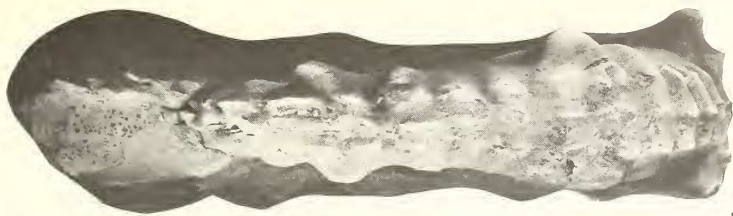
which siphonal tubercles greatly outnumber ventrolateral, whilst others show a more or less equal number; no two specimens agree in details of ornament.

Mature specimens show two broad types of decoration, but again no two specimens agree in detail. In the first group the umbilical bullae move outwards and fuse with the inner ventrolateral tubercles to form a strong to massive horn (if broad) or flange (if narrow). This supports a long, low, narrow outer ventrolateral clavus, and the front and rear of the horn strengthens into a pair of ribs which loop to the pair of siphonal clavi corresponding to each horn. Some specimens may develop a low siphonal horn at this stage and at the adult aperture up to three ventral ribs may appear between the primary ribs, although in other specimens these may be absent, the spaces between the major ribs being smooth. The second type is a more evolute form, retaining long, straight, distant flank ribs with bullae of variable strength, connected by weak or almost effaced ribs to strong conical ventrolateral horns which bear the outer ventrolateral clavus. A low siphonal ridge is present and there are pairs of clavi corresponding to the horns as well as additional clavi in the interspaces. This form differs most obviously from the first in the retention of bullae and in being somewhat larger.

The suture line is simple, with a massive, slightly incised, asymmetrically bifid E/L, narrow L and narrow, bifid L/U₂.

EXPLANATION OF PLATE 64

Figs. 1-3. *Collignoniceras woollgari* (Mantell). The lectotype of *Acanthoceras schlueterianum* (Laube and Bruder), from the Turonian of the White Mountain near Prague, Czechoslovakia. Pictures supplied through the courtesy of Dr. V. Houša (Prague).



3



2



1

Discussion. The above description is based upon the available English material, the large suite of specimens from Touraine and a few Czechoslovakian specimens before us. It must be stressed that no two specimens are alike and that description is inevitably generalized. Mantell's original figures of *Ammonites woollgari* give a clear and accurate representation of the juvenile form, but only suggest the very different adult form in general terms, better shown in Sowerby's (1828, p. 165; pl. 587, fig. 1) beautiful water colour and Sharpe's (1855, p. 27; pl. 11, figs. 1a-b) slightly inaccurate reconstruction.

The lectotype is, in fact, a moderately distorted composite internal mould only 130 mm in diameter, as can be seen from our photographs (Pl. 62, figs. 1-2; Pl. 63, fig. 9), showing no trace of sutures or any indications of how much is body chamber. In terms of the description given above, it falls into the first group of specimens. It is distinctive in the small size at which the massive horns are developed and the brevity of the stage with intercalated ribs.



TEXT-FIG. 2. *Collignonicerus woollgari* (Mantell) BMNH 88989a, a crushed specimen from the Turonian of the White Mountain, near Prague, Czechoslovakia.



TEXT-FIG. 3. *Collignoniceras woollgari* (Mantell) A, B, MNHP W14, 6778 (d'Orbigny Collection), from Poncé, Sarthe. A, tuffeau specimen agreeing closely with the type. Reduced $\times 0.5$ approx. C, D, MNHP 1946-19, from St. Maure de Touraine. A hypernodose adult of the first type. Reduced $\times 0.4$ approx.

At the beginning of the outer whorl the ribs bear strong umbilical bullae, strong conical inner ventrolateral and long, low, clavate outer ventrolateral tubercles and a strong elongate siphonal clavus. Between these long primary ribs are one or two shorter intercalated ribs which extend across the venter and bear small siphonal clavi. By 90 mm diameter these are lost and the ornament consists of an umbilical bulla which moves out progressively to occupy a mid-lateral position, linked by a broad rib to a massive inner ventrolateral horn which bears, at its base, the outer ventrolateral clavus. From this clavus two poorly defined, low, rounded ribs link to two ventral clavi.

The best-preserved horn on the lectotype is at 120 mm diameter, and here the bulla on the flank and the inner ventrolateral horn have merged into a massive horn bearing a much weakened outer ventrolateral clavus and subdued weakened ribs.

D'Orbigny (1841, p. 352, pl. 108, figs. 1-3) figured under the name *A. woollgari* a distinctive form which he subsequently (1850) named *A. vielbancii*; it is redescribed below as a junior subjective synonym of *Lecointerocras fleuriausianum* (d'Orbigny). D'Orbigny also described in *Paléontologie Française* a related form, *A. carolinus* (1841, p. 310, pl. 91, figs. 5-6), which he subsequently (1850) regarded as a synonym of *A. woollgari*, a view followed by most later authors. Sharpe (1855, p. 27, pl. 11, figs. 1a-b, 2a-b) clearly recognized the differences between young *woollgari* and *carolinus* ('... the French shell has twice as many ribs, is less compressed, and has the keel more completely separated from the ribs by two regular channels, than in our species'), and, as we describe below, the two are indeed specifically distinct.

Fritsch (1872) provided a very clear discussion of Mantell's species, and recognized three variants; his descriptions are loosely translated as follows:

(a) Typical form, which agrees exactly with the illustrations of Mantell and Sharpe. It has very strong tubercles on the siphonal side (pl. 4, figs. 1, 2).

(b) Form with slender ribs and weaker tubercles (pl. 3, fig. 2).

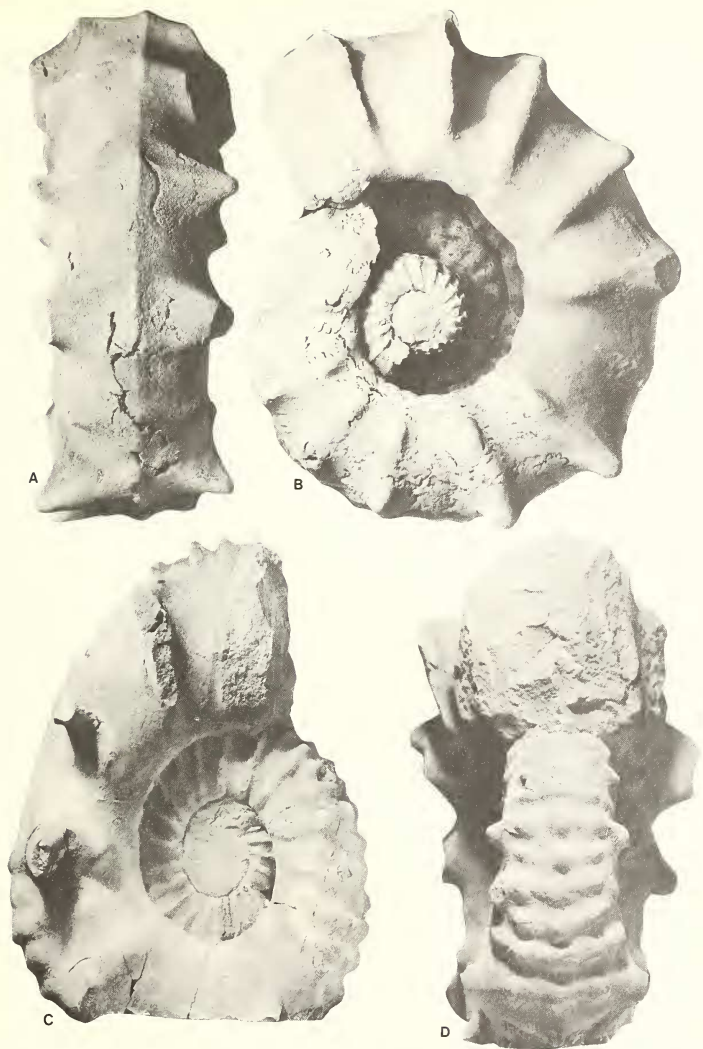
(c) More involute form with an inverse egg-shaped mouth opening. There are tubercles close to the umbilical seam, which remain there for a long period, and are stronger and more widely separated than in the typical form; there are only six, even on the inner whorl (pl. 3, fig. 1).

He also described a variety *lupulina* from Měcholup [Michelob] near Saatz, close to Prague (1872, p. 31, pl. 2, figs. 1, 2; pl. 15, fig. 6), which was said to be very similar to *woollgari* when young, but when old, has a different venter, large sparse tubercles and an almost square cross-section. It is, in fact, a *Mammites nodosoides* (Schlüter).

Schlüter (1872) figured a similar range of variants; his pl. 9, figs. 1-3 correspond to Fritsch's form c and his pl. 9, figs. 4-5 to the typical form. His variety (pl. 12, figs. 5-6) is, as he suggested, close to the *papale* group in many respects and it could well be referred to as *Collignoniceris* aff. *canthus* (Sornay).

Laube and Bruder (1887) reviewed a similar range of central European specimens but referred Fritsch's typical form (var. a) to a new species, *Acanthoceras schlueterianum*; they regarded the involute form (var. c) as typical *C. woollgari* and var. *lupulina* as a *Mammites*, which they renamed *Mammites michelobensis*. Petrascheck (1902) followed Laube and Bruder and described forms he called *woollgari*, *schlueterianum*, and aff. *woollgari*.

From our study of the type material and the Touraine populations, it is quite clear that no two adult *Collignoniceris* of these types are the same. The lectotype of *C. woollgari*, showing as it does an early loss of umbilical bullae, which move out to mid flank, fuse into ventrolateral horns, with much elongated outer ventrolateral clavi and subdued ribs looping to low siphonal clavi is clearly of the same general morphology as Fritsch's typical form (e.g. 1872, pl. 4, figs. 1-2) and the lectotype (here designated) of *Acanthoceras schlueterianum* (Laube and Bruder 1887, pl. 29, figs. 2a-b) (Pl. 64). It differs, however, in showing a decline in ventral ribs and clavi at only 90 mm diameter, whereas the Czechoslovakian examples retain umbilical bullae and intercalated ribs (particularly on the venter) to a much greater size and in consequence have a longer middle growth stage with umbilical bullae, conical inner ventrolateral and outer ventrolateral and siphonal clavi, like the specimen illustrated here (text-fig. 4 C-D), Fritsch's pl. 14, fig. 6 and Laube and Bruder's smaller paralectotype (1887, pl. 29, fig. 3). This stage is virtually suppressed in the lectotype of *C. woollgari*, which in these respects



TEXT-FIG. 4. *Collignonicer as woolgari* (Mantell) A, B. MNHP W22, 6778 (d'Orbigny Collection), from Ponce, Sarthe. An adult of the second type, retaining long ribs and moderately evolute coiling. Reduced $\times 0.4$ approx. C, D. BMNH 88988b, from the Turonian of the White Mountain, near Prague. Reduced $\times 0.5$ approx.

is atypical. Other specimens show that the intercalated ventral ribs are accompanied by weak flank ribs in middle growth but that there is great variation at this stage. The Touraine populations, which yield specimens that both match the lectotype of *C. woollgari* (text-fig. 3 A-B) and show every gradation to the other forms (Pl. 66, figs. 1-3; text-fig. 3 C-D) with strong intercalated ribs and tubercles, show that *C. woollgari* and *C. schlueterianum* should be treated as synonyms. Indeed, a specimen from Fritsch's own collection, now in the British Museum (Natural History) (no. 88989a) and labelled in his own hand 'Weisser Berg', the type locality of *C. schlueterianum* (text-fig. 2), exhibits the fusion of umbilical bullae with strong horns seen in the lectotype of *woollgari* but with more persistent intercalated ribs on the venter of the last whorl. The specimen is, furthermore, adult at only 150 mm, showing a rapid decline in ornament and loss of horns on the outer whorl.

In Germany (?), Czechoslovakia and Touraine (but not England where only one adult is known) this hypernodose, horned form, enormously variable in its adult ornament, is accompanied by the evolute, square-whorled forms which correspond to Fritsch's form C, to Laube and Bruder's 'typical form' and Petrascheck's *A. woollgari* + *A. cfr. woollgari*. Inner whorls of this type are inseparable from typical juvenile English *C. woollgari*, but again the variable adult whorls are quite distinctive, as Fritsch described, and as outlined above in our description; we conclude that these are probably sexual dimorphs.

C. woollgari var. *mexicana* (Böse) (1928, p. 262, pl. 11, figs. 11, 12) was originally described on the basis of a single, crushed specimen from the Turonian Ojinaga Formation equivalent, near Jimenez, Coahuila, Mexico, reillustrated here as Plate 65, figs. 1-3. Powell (1963) has redescribed this form (as *Selwynoceras mexicanum*) and discussed the intraspecific variation on the basis of large collections of fragmentary material. From large additional collections from the same area (OUM KT 1160-1183, 1200-1222, 1264-1313) and Chispa Summit, Jeff Davis County, Texas and specimens in the Adkins Collection (preserved in the Texas Memorial Museum) we conclude that it too is a synonym of *C. woollgari*. Juveniles, as Powell himself noted (op. cit., p. 1225), include individuals which cannot be separated from the English *C. woollgari* (Pl. 63, figs. 7-8), in addition to those which are more compressed, finely and densely ribbed.

Powell (1963, pl. 168, fig. 4) has figured a specimen in middle growth, showing the irregularly ribbed stage with development of inner ventrolateral horns as seen in Bohemian and Touraine specimens and we have other slender fragments which match Petrascheck's (1902, pl. 10, figs. 3a-b) juvenile *A. schlueterianum*. Larger fragments show a wide range of variation, from robust fragments having essentially equal numbers of inner and outer ventrolateral and siphonal tubercles to those with multiple ventral tuberculation. Adult body chambers show clear dimorphism, as in European material, the one form with flanges or flared horns produced by amalgamation of umbilical and ventrolateral tubercles, the other more quadrate, retaining to maturity umbilical bullae and distant ribs of variable strength. As can be seen from our and Powell's figures, distinction on the basis of the nature of the less complex suture, the finer ribbed juveniles and the coarse ornament of adults, by which Powell separated it from *C. schlueterianum*, cannot be upheld in the light of the variation seen in European specimens (not known to Powell); there is a clear overlap. We note the relatively frequent occurrence of individuals with flares and a compressed whorl, rarely seen in Europe, suggesting the Texas/Mexico material belongs to a local population more variable than their old world contemporaries.

EXPLANATION OF PLATE 65

Figs. 1-8. *Collignonoceras woollgari* (Mantell). 1-3, the holotype of *Prionotropis woollgari* (Mantell) var. *mexicana* Böse, from near Jimenez, Coahuila, Mexico. University of California, Berkeley, Collections. 4-6, BMNH 4863a, from the Middle Chalk near Lewes, Sussex. 7-8, a juvenile U.S. Western Interior specimen in the U.S. Geological Survey Collections, Denver, from USGS Mesozoic locality 21792, the mid-Turonian Carlile Shale of the Black Hills.



KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

The relationship of European specimens to the widely documented U.S. Western Interior material referred to *C. woollgari* has been complicated by the relatively few illustrations of English juveniles. Adults such as Meek's specimen (1876, pl. 7, fig. 1g) from the Black Hills, Dakota, would certainly fall within the concept of *C. woollgari* outlined here, although differing from the lectotype most obviously in the retention of umbilical bullae to a greater diameter. Dr. W. A. Cobban (Denver) has also shown us medium-sized specimens in which all ribs are long and the ventrolateral and siphonal clavi are equal in number, a feature uncommon in European material. American juveniles, described by Haas (1946) and Matsumoto (1965) amongst others, show a much wider range of variation than European material. This may be merely a consequence of the small number of juveniles known from Europe: indeed, the latter fall closest to Matsumoto's group E, one of the commonest forms in the Western Interior. Nevertheless, there is a clear overlap with European *C. woollgari*. The presence of similar individuals would also seem to preclude subspecific separation and we regard them as conspecific, but with a different population structure. Specific differentiation of the American fauna from their European contemporaries occurred later, with the evolution of the early members of the *Prionocyclus hyatti* group.

W. A. Cobban (*in litt.*) has suggested to us that forms with more siphonal than ventral nodes pre-date those in which the numbers are equal in the U.S. Western Interior, but, as we do not know the precise horizon of the holotype of *woollgari* in relation to these, we prefer to unite them here, leaving revision of these faunas to Dr. Cobban.

According to Matsumoto (1959, p. 107; 1965, p. 16, pl. 3, figs. 3-4) *C. woollgari bakeri* Anderson is a subgroup of *C. woollgari* that characterizes the north Pacific region. All described specimens are small, compressed, evolute *Subprionocyclus*-like densely ribbed shells, close to subgroup D of *C. woollgari* of Matsumoto (1965) from the U.S. western Interior, but more evolute and with less prorsiradiate ribs. These differences probably do not merit separation, but without more and adult specimens further comment is inadvisable.

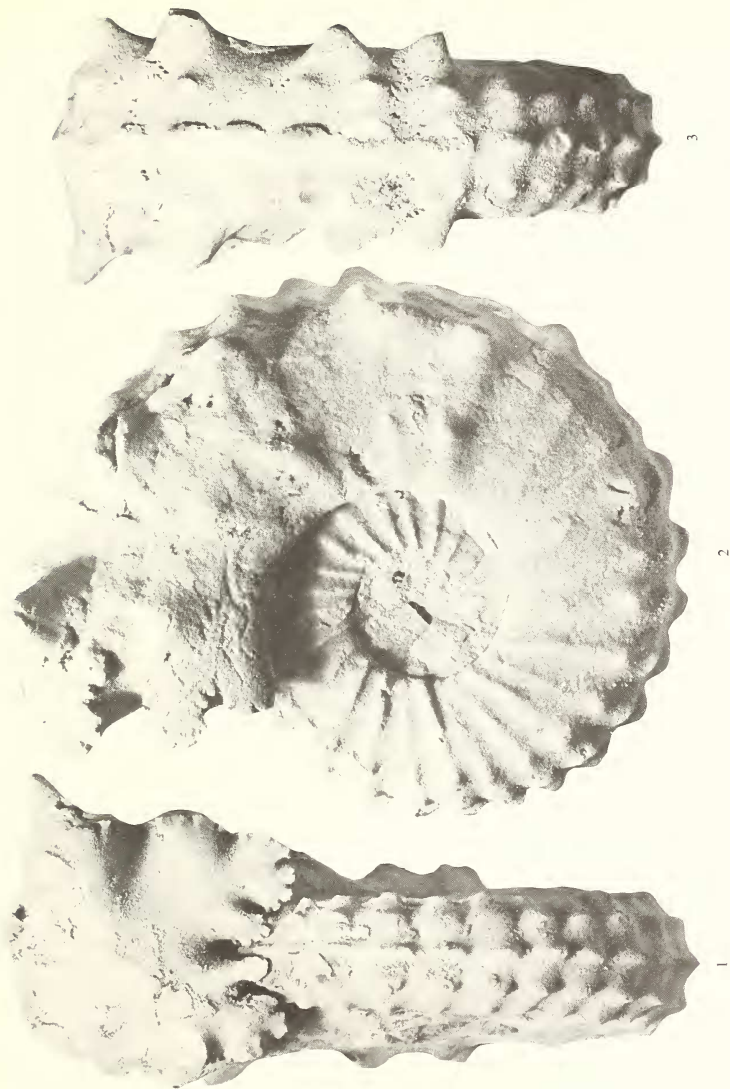
C. woollgari is easily separated from the remaining species of the genus. *C. carolinum* (d'Orbigny) (p. 574) is usually more densely ribbed and even in sparsely ribbed juveniles (Pl. 68, fig. 11) the ribs are low and subbudd rather than bar-like. Adults are quite distinct; *C. carolinum* reaches maturity at only 100-120 mm diameter, never develops the coarse umbilical bullae, ribs, and horns of *woollgari*, nor the complex looped ventral ornament. Instead, it remains compressed and flat sided, with weak ribs and tubercles and a persistent, crenulated siphonal ridge. *C. canthus* (Sornay) (p. 582) has coarsely and sparsely ribbed and tuberculate inner whorls but a virtually smooth body chamber with only faint ribs and many tiny siphonal tubercles. *C. turoniense* (Sornay) (p. 584) has similarly coarsely ornamented early whorls, is adult at a much smaller size with more massive whorls, coarse sparse bullae, weak ribs and ventrolateral horns and the inner ventrolateral tubercles disappear at an early stage.

There is a closer resemblance to *C. papale* (d'Orbigny) (p. 578) but here juveniles have fewer, coarser ribs with strong bullae displaced well out from the umbilical shoulder, with much more prominent inner ventrolateral tubercles. In middle growth *C. papale* lacks the prominent ventrolateral horns of many *C. woollgari* and the inner and outer ventrolateral tubercles merge into a pinched clavus, retained to much greater diameters in *C. woollgari*. Other differences are noted on p. 582.

C. boreale (p. 586) is a genuinely small form, showing adult features at only 100 mm diameter in the holotype. It has narrow, distant ribs and retains umbilical bullae to the end of the phragmocone, showing early development of flared ventrolateral flanges and traces of looped ventral ribs.

EXPLANATION OF PLATE 66

Figs. 1-3. *Collignonicerus woollgari* (Mantell). Adult phragmocone showing intercalation of flank and ventral ribbing, multiple ventral tuberculation and early stages of horn development. MNHP W10, from either Poncé (Sarthe) or Bourré (Loir-et-Cher).



KENNEDY, WRIGHT and HANCOCK, *Collignoniceratid* ammonites

Occurrence. Few *C. woollgari* from England are well dated. Through the courtesy of the Director of the Institute of Geological Sciences and Mr. C. J. Wood we have been able to examine the precisely positioned material from the Leatherhead (Fetcham Mill), Surrey, Borehole (Gray 1965). Here *C. cf. woollgari* occurs at a depth of 570' 6" (GSM.WN 1979-80, 1982-3), 73' 1" (22.28 m) above the base of the Melbourn Rock and 17' 6" (5.33 m) above a specimen of ?*Mytiloides hercynicus*; at 535' 10" (GSM.WN 1942), 12' (3.66 m) above the level of large *Inoceramus* of *inequivalvis* type, and at 518' 9" (GSM.WN 1900, 1901), 26' 9" (8.15 m) below specimens of *Mytiloides* sp. and *I. cf. apicalis* (inoceramids determined by Mr. P. Woodroof). This range, through 51' 9" (15.8 m) of section, includes the top of the *Inoceramus labiatus*/*Orbirhynchia cuvieri* and the lower part of the *Terebratulina lata* Zones. Other English specimens have been recorded from both *labiatus* and *lata* Zones. Specimens from Sussex, the type area, come mostly from the Lewes region. One specimen (BMNH C30394) is said to be from Mount Caburn; unfortunately the classic pit here extends from the Melbourn Rock to basal Upper Chalk (*labiatus-planus* Zones).

Specimens from the upper part of the *lata* Zone of Surrey (e.g. WW 14792-4, 16682), and OUM K 10273, K 10275-6 from no more than 5 m below the top of the Chalk Rock at Fognam, Berkshire, indicate the upper limit of its relatively long range. This is confirmed by occurrences in Sarthe and Touraine through the middle and upper part of the Tuffeau Blanc, in the St. Cyr-en-Bourg Fossil Bed, Bourré and Poncé faunas. In the United States the species occurs rarely in the top of Cobban and Scott's (1972) *Mammites nodosoides* Zone (Cobban *in litt.*) and overlaps with the succeeding *Prionocyclus hyatti* (Powell, 1963).

Elsewhere the species is known to occur widely in Europe, the U.S.S.R. west to Transcaspia, Japan, California and Oregon, Texas, Mexico, the U.S. Western Interior and northern Australia.

Collignoniceras carolinum (d'Orbigny)

Plate 68, figs. 1-11; Plate 76, figs. 1-2; text-figs. 1b, 5

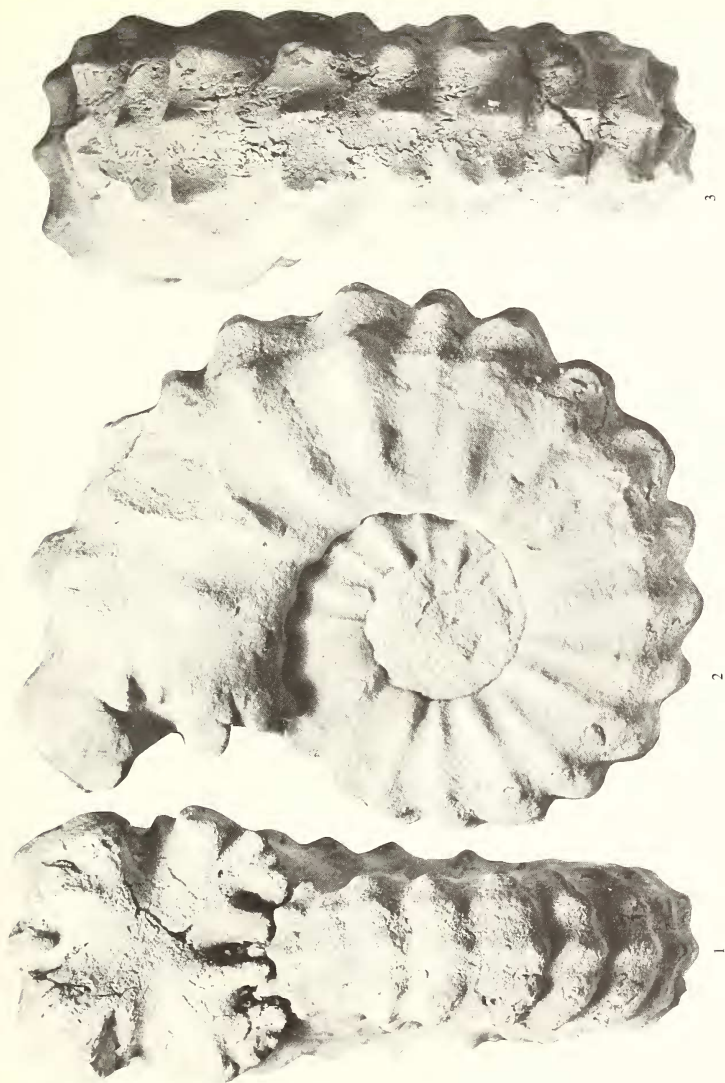
- 1841 *Ammonites Carolinus* d'Orbigny, p. 310, pl. 91, figs. 5-6.
- 1850 *Ammonites Woollgarii* Mantell; d'Orbigny, p. 189 (*pars*).
- 1860 *Ammonites Carolinus* d'Orbigny; Pictet and Campiche, p. 316.
- 1872 *Ammonites carolinus* d'Orbigny; Schlüter, p. 27, pl. 9, fig. 6.
- 1881 *Ammonites Carolinus* d'Orbigny; Windmüller, p. 33.
- ?1887 *Acanthoceras Carolinum* d'Orbigny; Laube and Bruder, p. 232, pl. 27, fig. 1.
- 1902 *Prionotropis carolinus* d'Orbigny; Petrascheck, p. 152.
- ?1912 *Prionotropis woollgari* var. *carolinus* (d'Orbigny); Arkhangelsky, p. 72, pl. 3, figs. 20-22 (*vide* Arkhangelsky, 1916).
- 1925 *Prionotropis carolina* (d'Orbigny); Diener, p. 156 (*pars*).
- 1977 *Collignoniceras* (*Collignoniceras*) *carolinum* (d'Orbigny); Hancock, Kennedy and Wright, p. 156.

Types. D'Orbigny's original account of this species is as follows: 'Je l'ai recueillie en place aux Martrous, près de Rochefort (Charente-Inférieure), dans la craie que je rapporte aux grès verts supérieurs ou aux craies chloritées. Elle y est rare à l'état de moule. M. d'Archiac l'a aussi rencontrée à Sainte-Maure (Indre-et-Loire), dans le même couche.' By 1850 d'Orbigny had concluded that *carolinus* was a synonym of *woollgari* (*Prodrôme*, p. 189), and in consequence no specimens are represented in his collections under the name *carolinus*. Under *Ammonites woollgari*, however, there is a specimen from Martrous with the label 6778a which is clearly the basis of the original figure (Pl. 68, figs. 4-8), and this is here designated lectotype of the species.

Other specimens studied. OUM KZ 747, from the St. Cyr-en-Bourg Fossil Bed, Champignonnière les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay, Maine-et-Loire. An unregistered specimen in de Grossouvre's collection (Sorbonne, Paris) from either Poncé (Sarthe) or Bourré (Loir et Cher). MNHP W8, from an unknown locality in the Tuffeau. WW 14791 from the *Terebratulina lata* Zone, Mickelham Bypass, Surrey.

EXPLANATION OF PLATE 67

Figs. 1-3. *Collignoniceras woollgari* (Mantell). Adult phragmocone of sparsely and robustly ribbed variant with equal numbers of umbilical, ventrolateral and siphonal tubercles. MNHP W2. 1904-32. 'Le Mans, Sarthe'.



KENNEDY, WRIGHT and HANCOCK, *Collignoniceratid* ammonites

Dimensions

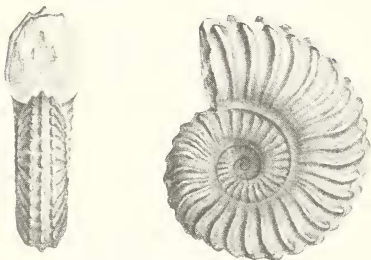
	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Lectotype					
MNHP 6778a	46.0 (100)	14.0 (30)	15.0 (33)	0.93	16.7 (36)
Sorbonne spec.	108.5 (100)	28.2 (26)	37.5 (35)	0.75	34.3 (32)

Description. The lectotype from Martrous (Charente-Maritime) is a fragment with juvenile body chamber preserved in calcarenite typical of the Calcaires à Céphalopodes of the Rochefort area. Coiling is relatively evolute, with a broad, shallow umbilicus (36% of the diameter). The umbilical wall is low and rounded. The whorl section is compressed (whorl breadth to height ratio is approximately 0.93), with flattened, convergent sides, the maximum breadth close to the umbilical shoulder and the venter fastigate. Ornament consists of strong, dense, narrow ribs (nineteen on last half-whorl), arising at the umbilical shoulder without clear bullae after the first two visible ribs. They are straight or slightly flexed and prorsiradiate on the inner flank, curving strongly forwards across the ventrolateral shoulders and venter. Single, shorter intercalated ribs occur commonly on the early part of the specimen but there are only two in the last half-whorl. The ribs are strengthened into distinct if small inner ventrolateral tubercles at the beginning of the body chamber, but these are lost beyond a diameter of about 34 mm. There are well-marked outer ventrolateral clavi, connected by forwards-directed weak ribs to elongate siphonal clavi borne on a low, rounded keel. Other specimens show both denser and sparser ribbing of the same style, as in other *Collignonicer* juveniles (Pl. 68, figs. 10, 11).

Body chambers show the species to have been adult at small diameters (100–120 mm). The adult whorls are compressed (whorl breadth to height ratio as little as 0.75) with gently inflated inner, and flattened outer flanks, with a fastigate venter. Ornament consists of numerous (about thirty) rather low, rounded, prorsiradiate ribs, arising at the umbilical shoulder without bullae and flexed strongly forwards, concave on the outer flank and ventrolateral shoulder, where they bear blunt, clavate tubercles. The ribs are narrow as they sweep forwards from these to long siphonal clavi. Rarely ribs branch from the umbilical seam or are intercalated, so that there are more siphonal clavi than long ribs.

The sutures are indifferently exposed (text-fig. 1B), but are typically collignoniceratid, with broad, simple, bifid elements.

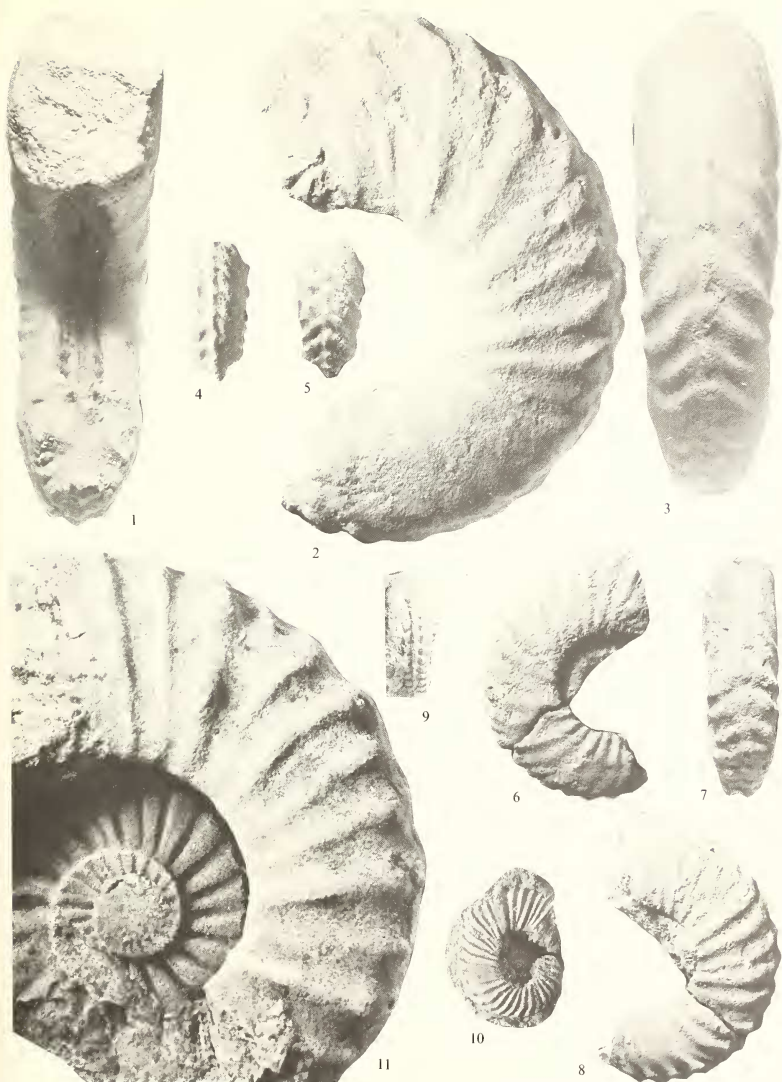
Discussion. D'Orbigny's figure is partly idealized: in addition the figure lacks the abrupt start of the ribs at the umbilical shoulder, shows too many short ribs and makes the species appear too inflated (text-fig. 5). Pictet and Campiche (1860, p. 316) and de Grossouvre (1894, p. 75) regarded this species as a juvenile *C. woollgari*, but Sharpe (1855, p. 27) had already noted that 'the French shell has twice



TEXT-FIG. 5. *Collignonicer carolinum* (d'Orbigny). Copies of d'Orbigny's original figures (1841, pl. 91, figs. 5–6).

EXPLANATION OF PLATE 68

Figs. 1–11. *Collignonicer carolinum* (d'Orbigny). 1–3, SP, de Grossouvre Collection, probably from Bourré (Loir-et-Cher). 4–8, the lectotype, MNHP 6778a, from the Calcaire à Céphalopodes of Martrous, near Rochefort (Charente-Maritime). 9–10, OUM KZ 747, from the St. Cyr-en-Bourg Fossil Bed, Champignonnière les Rochains, south of Saumur and east of Montreuil-Bellay (Maine-et-Loire). 11, MNHP, from an unknown locality in the Tuffeau Blanc de Touraine.



KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

as many ribs, is less compressed, and has the keel more completely separated from the ribs by two regular channels'. Schlüter (1872, p. 27) maintained the species, as did Laube and Bruder (1887, p. 232), although their specimen is only doubtfully referable to it. Meek (1876, p. 457) regarded d'Orbigny's *Ammonites bravaisianus* as the juvenile of *carolinum*, which he in turn treated as a synonym of *woollgari*.

In the last 50 years the name has dropped out of currency. The most recent reference was by Matsumoto (1971, p. 131) who upheld the view that it was possibly an immature example of *C. woollgari* in which the appearance of strong distant ribs was delayed, in this respect being intermediate between *C. woollgari woollgari* and *C. woollgari bakeri*.

C. carolinum is in fact quite distinct from *C. woollgari*. As early authors noted, the type of the species is consistently more finely and densely ribbed than European *C. woollgari* and at comparable diameters the ribbing is much more subdued and the ventral tuberculation finer. Other examples before us show much sparser ribbing (Pl. 68, fig. 11), but even here the ribbing is more subdued. When adult the species are very distinct; *C. carolinum* reaches maturity at only 100–120 mm and never develops the coarse umbilical bullae and ribs, the massive ventrolateral horns or the complex looped ventral ribbing and tubercles of *C. woollgari*.

The delicately ribbed inner whorls immediately distinguish the species from the grossly tuberculate young of *C. canthus*, *C. turoniense* and *C. papale*. Adult *C. canthus* are broader whorled and retain massive bullae and ribs, whilst *C. papale* has strong ribs with conspicuous looping as well as being more inflated. The feebly ornamented body chamber of *C. turoniense* is superficially similar, but is much broader, virtually lacks ribs but has a row of small siphonal tubercles.

C. boreale, although adult at a similarly small diameter, has much coarser ribbing when young, and develops distant coarse flared ribs when adult.

The confusion of *C. carolinum* with *C. woollgari* stems from the similarity of the former to finely ribbed forms of the latter known from Japan and the United States. These have been described by Haas (1946) as *Prionotropis woollgari* vars. *regularis* and *tenuicostata*, and by Matsumoto (1965) as his Group B of *C. woollgari*. These finely ribbed forms are distinguished from the type of *C. carolinum* in always developing relatively coarse ribs at a diameter of 20 mm or less and by ribs that are sharp rather than subdued, straight rather than flexuous.

Occurrence. This is a rare species. Apart from the Touraine records above, it is known in France from the environs of La Rochelle in Charente; in England from the *Terebratulina lata* Zone of Surrey; in north Germany, Bohemia and Turkestan.

Collignoniceras papale (d'Orbigny)

Plate 69, figs. 1, 2; Plate 70, figs. 3–5; text-figs. 1c, 6–7

- 1841 *Ammonites Papalis* d'Orbigny, p. 354, pl. 109, figs. 1–3.
- 1850 *Ammonites papalis* d'Orbigny, p. 189.
- 1887 *Acanthoceras papaliforme* Laube and Bruder, p. 237, pl. 27, figs. 3–4.
- 1925 *Prionotropis papalis* d'Orbigny; Diener, p. 156.
- 1925 *Prionotropis papaliformis* Laube and Bruder; Diener, p. 156.
- 1977 *Collignoniceras* (*Schwynoceras*) aff. *papale* (d'Orbigny); Hancock, Kennedy and Wright, p. 156.
- 1977 *Collignoniceras* (*Schwynoceras*) gr. *papale* (d'Orbigny); Hancock, Kennedy and Wright, p. 156.

Holotype. By monotypy the specimen in the Requiin Collection (Musée d'Avignon), presumed to come from the 'craie tuffeau ou chloritée du département de Vaucluse' (d'Orbigny 1841, p. 356). We have not seen the holotype, but d'Orbigny's figure (text-fig. 6) is little more than two-thirds natural size.

Specimens studied. There is a series of specimens in the Muséum d'Histoire Naturelle, Paris; five recorded in the d'Orbigny Collection as coming from Montrichard (Loir-et-Cher), reg. no. 6780; MNHP W.9, unlabelled but probably from Bourré; MNHP '3', from Montrichard; MNHP 'A' 'B' 'D' 'E' from Bourré. MNHP 'F' unlocalized but from the Tuffeau de Touraine.

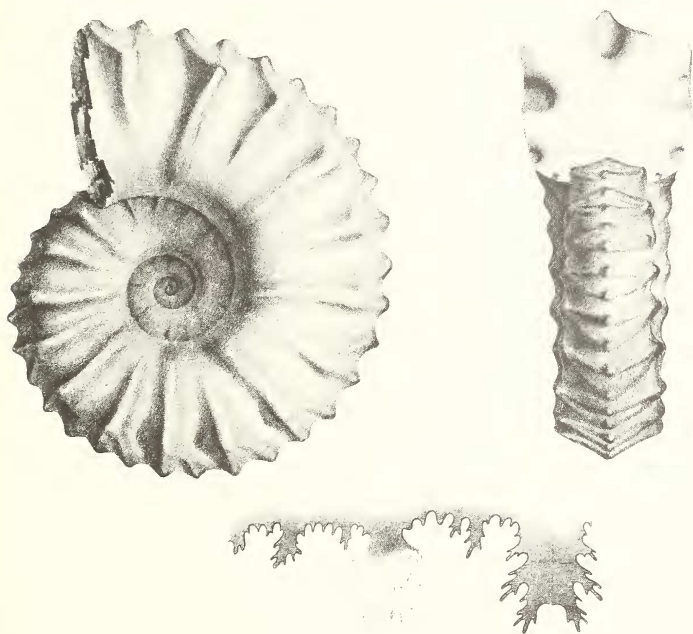
There are several unregistered specimens in the de Grossouvre Collection, housed in the Sorbonne, from either Bourré or Poncé; a specimen labelled Bourré showing the inner whorls; and a small body chamber, also unregistered, is labelled Bourré.

OUM KZ 738 and 745 are from the St. Cyr-en-Bourg Fossil Bed, Champignonnière les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay, Maine-et-Loire.

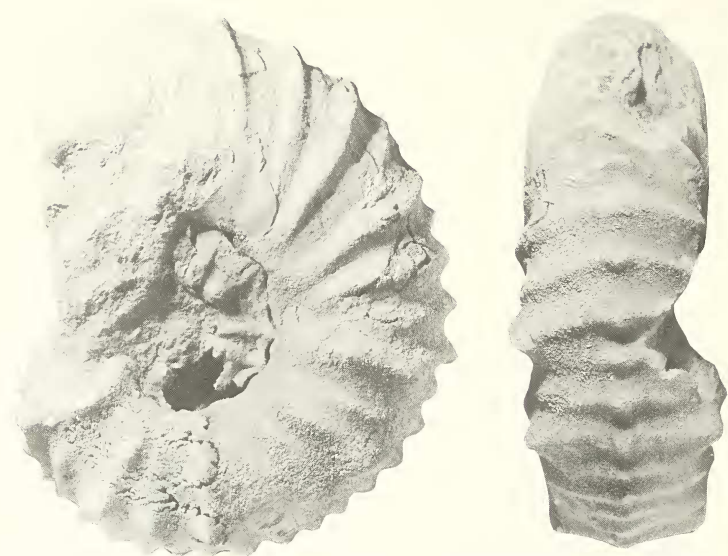
Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
MNHP W '9'	112.3 (100)	36.4 (32)	41.8 (37)	0.87	— (—)
MNHP 'B'	111.7 (100)	— (—)	41.0 (37)	—	39 (35)
SP, de Grossouvre	160.0 (100)	51.0 (32)	60.0 (37)	0.85	53.0 (33)
Collection	at 135.0 (100)	54.5 (40)	58.0 (43)	0.94	44.5 (33)
SP, Bourré	120.0 (100)	40 (33)	46.0 (38)	0.87	38.8 (32)

Description. The inner whorls of this species are best displayed by the specimen from Bourré in the Sorbonne Collections illustrated as Plate 70, figs. 3–5. Up to a diameter of 55 mm the coiling is relatively evolute, with a medium-sized umbilicus (30% of diameter), quite shallow, showing on the mould a rounded and undercut wall.



TEXT-FIG. 6. *Collignoniceras papale* (d'Orbigny). Copies of d'Orbigny's original figures (1841, pl. 109, figs. 1–3) of the holotype from the 'Craie Chloritée ou Craie Tuffeau du département de Vaucluse'. The specimen is said to be 120 mm in diameter.



TEXT-FIG. 7. *Collignoniceras papale* (d'Orbigny). Adult specimen in the Sorbonne Collections (de Grossouvre Collection), from either Poncé or Bourré. Reduced $\times 0.6$.

The intercostal whorl section is slightly compressed (Wb:Wh is 0.9), with convergent flanks, broadly rounded ventrolateral shoulders and a flattened venter. The costal section is polygonal, with the greatest breadth at the umbilical bulla. There are thirteen umbilical bullae per whorl. At the smallest diameter visible, they are very elongate and lie close to the shoulder. With growth the maximum development migrates outwards leaving a weak development only at the umbilicus, with the main bulla low on the flank. Broad, strong, straight, slightly prorsiradiate ribs arise from the bullae, cross the flanks and connect to strong, conical inner ventrolateral tubercles, from which a broad, strong rib sweeps forwards to strong outer ventrolateral clavi. These are in turn connected to elongate siphonal clavi by a broad, low, forwardly directed rib. Between long ribs there are some four intercalatories, usually with outer ventrolateral and siphonal clavi only.

From 50 mm onwards the ribs connecting the inner and outer ventrolateral tubercles strengthen and at 55 mm they have fused into blunt, oblique clavi.

During middle growth, ornament consists of distant, weak to strong umbilical bullae, displaced progressively outwards to a low or even mid flank position (not shown on d'Orbigny's figure), which give rise to one or rarely a

EXPLANATION OF PLATE 69

- Figs. 1-2. *Collignoniceras papale* (d'Orbigny). SP, from Bourré (Loir-et-Cher) (Saemann Collection).
 Figs. 3-4. *Collignoniceras woollgari* (Mantell); BMNH 5742a-b, paralectotypes from the Middle Chalk near Lewes, Sussex.



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pair of narrow, straight, prorsiradiate ribs, whilst single intercalated ribs arise at varying levels on the flank. All ribs bear a pinched ventrolateral bulla (if weak) or horn (if strong). These are commonly limited before and behind by narrow ribs, which loop across the venter, although the extent of this looping varies widely from specimens in which it predominates (Pl. 70, fig. 4) to those where it is simple (Pl. 69, fig. 1).

Over the last half whorl of adult body chamber the tubercles decline markedly, leaving rather weak, relatively crowded ribs without umbilical bullae, a weak, oblique to radially elongate ventrolateral tubercle (which may disappear several ribs before the aperture) and a small blunt siphonal tubercle (text-fig. 7).

The suture is rather simple, with a broad E which tapers apically; broad, rather simply incised and asymmetrically bifid E/L, narrow L and smaller, bifid L/U₂. U₂ is small (text-fig. 1c).

Discussion. The material before us shows considerable variation in the relative strength of umbilical bullae and ribs, as well as being adult (and showing typical decline in ornament) over a range of 120–180 mm diameter. Nevertheless, it forms a compact species group.

Collignonicer as canthus is immediately distinguishable on the basis of its massively tuberculate inner whorls and feebly ribbed, almost smooth body chamber with many fine ventral clavi, as discussed on p. 584. There are closer similarities to *C. turoniense*, but here the massive bullae of the inner whorls and general dominance of tuberculation over ribbing is diagnostic, as discussed on p. 586.

There are also similarities between juveniles of *C. papale* and *C. woollgari*, but *papale* have fewer, coarser ribs (compare Pl. 69, figs. 3–4 and Pl. 70, fig. 3), with strong bullae displaced well out from the umbilical shoulder and much more prominent inner ventrolateral tubercles. *C. papale* in middle growth is more sharply and distantly ribbed and does not have the prominent ventrolateral horn of many *woollgari*. The inner and outer ventrolateral tubercles merge into pinched, radially elongated clavi during middle growth in *papale*; in *woollgari* they are distinct to a much greater size. The venter of *C. papale* may bear strong narrow looped ribs at a much earlier stage than *woollgari* and is mature at a much smaller diameter, never developing the spectacular distantly ribbed, hypernodose body chamber of the latter.

C. carolinum has some common features, particularly its rather small adult size. It differs in having densely and evenly ribbed inner whorls without strong bullae, and a compressed flat-sided body chamber without the umbilical bullae, strong ventral tubercles and broad venter with looped ribbing of *papale*.

C. papaliforme (Laube and Bruder) (1887, p. 237; pl. 27, figs. 3–4), from the Turonian Greensand of the White Mountain, near Prague, is no more than a deformed *C. papale*.

Occurrence. This is a relatively long-ranging species in the Tuffeau Blanc of Touraine, first appearing in the St. Cyr-en-Bourg Fossil Bed of the Saumur region, and also occurring at Montrichard, Bourré, and Tourtenay (Deux Sèvres). Elsewhere in France there are records from Uchaux (Vaucluse). The species also occurs in the Turonian of Czechoslovakia.

Collignonicer as canthus (Sornay)

Plate 73, figs. 1–4

- 1951 *Ammonites canthus* d'Orbigny in litt.; Sornay, p. 629, text-figs. 1c, 2.
 1955 *Ammonites (Selwynoceras) canthus* d'Orbigny ms; Sornay, fiche 8, figs. 1–2.
 1977 *Collignonicer as (Selwynoceras) canthus* (Sornay ex d'Orbigny ms); Hancock, Kennedy and Wright, p. 156.

EXPLANATION OF PLATE 70

Figs. 1–2. *Collignonicer as boreale* (Warren). Cast of the holotype, Alberta Museum Collections no. CT 468, from the basal beds of the Smoky River Shale, Grimshaw, near Peace River, Alberta.

Figs. 3–5. *Collignonicer as papale* (d'Orbigny), nucleus, showing coarse juvenile ornament; SP, from Bourré (Loir-et-Cher).



KENNEDY, WRIGHT and HANCOCK. *Collignoniceratid* ammonites

Holotype. By monotypy the original of Sornay's (1951), text-figs. 1e, 2, from the Tuffeau Blanc de Touraine of Bourré (Loir-et-Cher), Muséum d'Histoire Naturelle, Paris, no. 6793.

<i>Dimensions</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype					
MNHP 6793	126 (100)	40.8 (32)	49.5 (39)	0.82	48.6 (39)

Description. The holotype and only known specimen consists of the internal mould of a body chamber 126 mm in diameter and an external mould of the umbilicus of the inner whorls. The umbilical mould shows that the species bore seven massive conical umbilical bullae at the smallest diameter visible (Pl. 73, fig. 3) and a similar number on the following whorl, supplemented by three ribs lacking bullae but extending to the umbilicus. From the bullae arose rather strong ribs, usually in pairs, with occasional shorter intercalated ribs. The external mould of the dorsum of the last part of the phragmocone shows each of these ribs to have borne a conical ventral tubercle whence arose a pair of feeble ribs, connecting to feeble siphonal tubercles in the same looped style seen in *Collignoniceras papale* (d'Orbigny).

The body chamber shows coiling to have been moderately evolute, with a small umbilicus comprising 39% of the diameter. The umbilical wall is low and rounded, the flanks flattened and convergent, with a low fastigiate venter which tends to become rounded towards the aperture. The maximum whorl breadth is low on the flanks, close to the umbilical shoulder.

On the early part of the body chamber there are weak umbilical bullae, which give rise to pairs of low, broad, radial ribs, almost insensible save to touch, as are occasional shorter, intercalated ribs. The ribs become progressively finer, denser and more subdued towards the mature aperture, and are gently flexed.

All ribs bear faint, low, rounded ventrolateral clavi which give rise to pairs of low ribs which loop forwards and across the venter to low siphonal clavi linked into a semi-continuous serrated ridge.

The rather poorly preserved sutures of the holotype are approximated, confirming it as an adult.

Discussion. The strongly ornamented inner whorls of *C. canthus* place it in the same group as *C. papale* and *C. turoniense*. It differs from both of these in the marked decline and virtual disappearance of ornament on the outer whorl. We have seen no intermediate forms. *C. carolinum* (d'Orbigny) has delicately and densely ribbed, rather than coarsely bullate inner whorls. The body chambers of the two are more similar, especially in the marked decline in ornament, but *carolinum* is much more compressed and flat-sided, the ribs are stronger, with quite thick ventral development, and stronger siphonal clavi.

Occurrence. *C. canthus* is known only from the Tuffeau Blanc de Touraine of Bourré.

Collignoniceras turoniense (Sornay)

Plate 71, figs. 4-5; Plate 72, figs. 1-3

1951 *Prionotropis turoniense* Sornay, p. 630; pl. 21, figs. 1-3.

1977 *Collignoniceras* (*Sehwynoceras*) *turoniense* (Sornay); Hancock, Kennedy and Wright, p. 156.

Holotype. MNHP unregistered, Peron Collection, from Bourré (Loir-et-Cher), by monotypy.

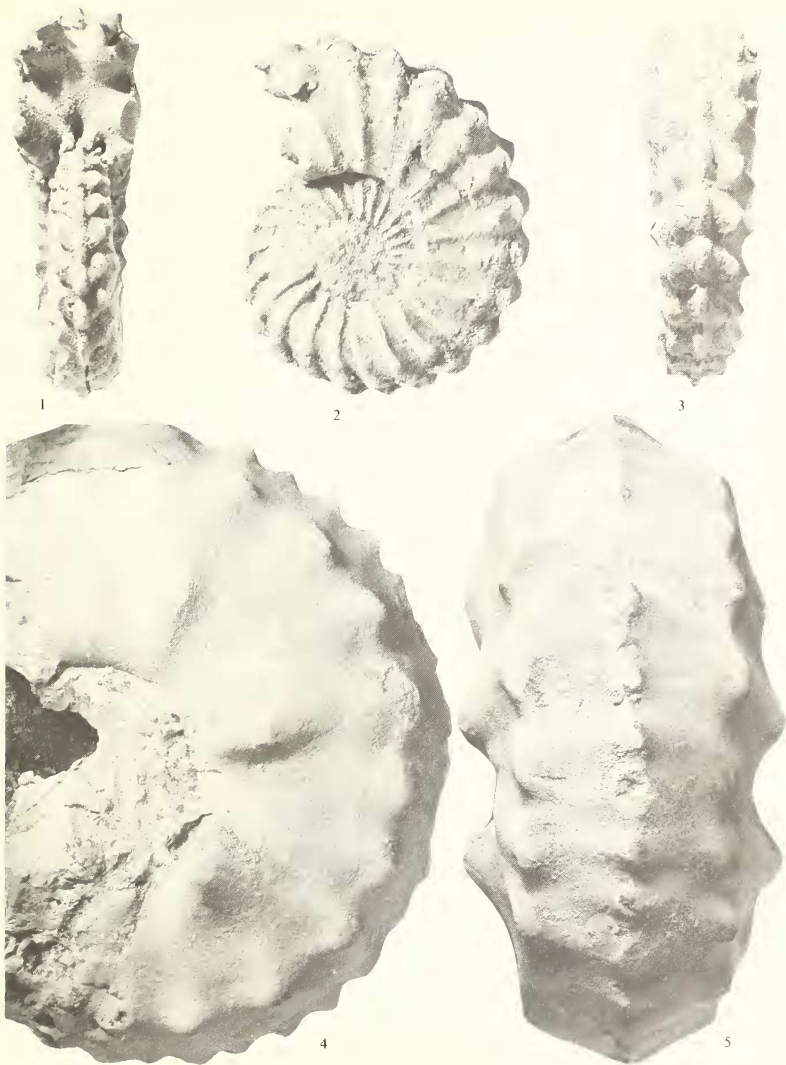
Other specimens studied. MNHP 'A', from Bourré, and two unregistered specimens in the de Grossouvre Collection (Sorbonne, Paris), probably from Bourré.

<i>Dimensions</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype	120 (100)	48 (40)	48.3 (40)	1.0	— (—)
MNHP 'A'	107 (100)	52 (49)	44 (41)	1.18	34.5 (32)
Sorbonne, 1	125 (100)	43.5 (35)	48.5 (39)	0.9	34.5 (28)
	at 107.5 (100)	52.5 (49)	43.5 (43)	1.2	23.0 (21)

EXPLANATION OF PLATE 71

Figs. 1-3. *Collignoniceras woollgari* (Mantell) FSR C273, from Poncé, Sarthe.

Figs. 4-5. *Collignoniceras turoniense* (Sornay), the holotype, MNHP, Peron Collection, from Bourré (Loir-et-Cher).



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Description. All known specimens are adults, with two-thirds of the last whorl being body chamber, and none show the early whorls. Coiling is involute on the phragmocone, becoming relatively evolute at maturity, with a deep umbilicus. On the phragmocone the whorl section is depressed, with convergent flanks and a fastigiate venter intercostally. The costal section is even more depressed, the greatest breadth being at the umbilical bullae, and subcarinate. There are five massive blunt conical umbilical nodes per whorl. These give rise to groups of two or three broad, low ribs, with additional ribs intercalated low on the flank between the groups. At the smallest diameters visible these bear blunt conical inner ventrolateral tubercles and small clavate outer ventrolaterals, with a broad low rib connecting them to stronger siphonal clavi borne on a blunt keel. On the last part of the body chamber the intercalated ribs decline, the inner and outer ventrolateral tubercles combine into a blunt transversely elongate tubercle, which gives rise to pairs of ribs which loop to strong siphonal clavi, which become first rounded, then transversely elongate. Some short ventral ribs with a siphonal tubercle are intercalated, to give a serrated blunt keel; there are three to five siphonal nodes to each pair of umbilicals.

On the body chamber the umbilical nodes decline in strength and disappear towards the aperture; intercalated ribs are lost and the primary ribs weaken and become irregular and closely spaced. There are irregularly spaced, clavate ventrolateral nodes, which also decline towards the aperture, with many more ventral ribs and siphonal tubercles than ventrolateral.

The body chamber uncoils markedly and the shell becomes much more evolute as a result. Whorl height: breadth ratio decreases, so that the aperture appears relatively constricted.

None of the specimens shows the suture well but they appear to have comprised broad, plump, rather simple bifid lobes and saddles.

Discussion. The inner whorls of *Collignonicerus turoniense* are easily distinguished from those of *C. woollgari* and *C. carolinum*, which are densely and evenly ribbed by comparison, lacking massive bullae. In middle growth, *C. turoniense* has a much more massive whorl, broad and low rather than narrow ribs and stronger ventrolateral than umbilical nodes. The adults are quite distinct (compare Pl. 62, figs. 1-2 and Pl. 71, figs. 4-5).

C. canthus has similar inner whorls, but becomes virtually smooth in middle and later growth, lacking massive umbilical bullae and strong ventrolateral tubercles.

C. papale juveniles (Pl. 70, figs. 3-5) have many more (typically 9-11) and smaller umbilical bullae, narrow and widely spaced ribs and more markedly clavate ventrolateral and siphonal tubercles. In middle and later growth the differences between the two lie in the predominance of tuberculation in *C. turoniense* and of ribbing in *C. papale*, the latter having the bullae displaced outwards to a lower flank position and strong, narrow, well-differentiated ventral ribs looping between the ventrolateral and siphonal tubercles with intercalatories.

C. carolinum is compressed, parallel-sided and feebly ribbed without strong bullae in middle and later growth.

Occurrence. *C. turoniense* is known only from the Tuffeau Blanc de Touraine of Bourré.

Collignonicerus boreale (Warren)

Plate 70, figs. 1-2

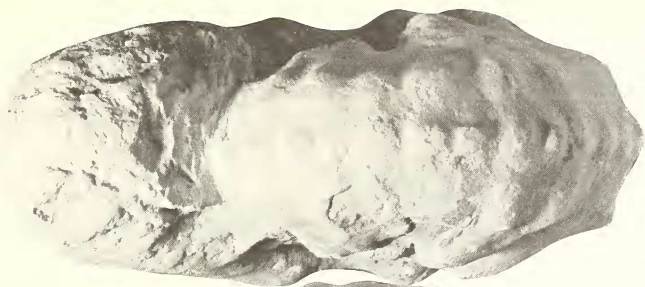
1930 *Prionotropis borealis* Warren, p. 25, pl. 3, figs. 1-4; pl. 4, fig. 1.

1940 *Schwynoceras borealis* Warren; Warren and Stelck, p. 151.

Types. The holotype is the original of Warren 1930, pl. 3, fig. 1, University of Alberta Museum Collections no. CT 468. Paratypes are CT 469-76, all from the basal beds of the Smoky River Shale, Grimshaw, near Peace River, Alberta.

EXPLANATION OF PLATE 72

Figs. 1-3. *Collignonicerus turoniense* (Sornay) SP, de Grossouvre Collection, probably from Bourré (Loir-et-Cher).



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Description. The holotype, a cast of which is before us, is a slightly distorted mould retaining traces of shell and consists of half a whorl of body chamber and one quarter of a whorl of phragmocone with the following dimensions:

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
costal	92.5 (100)	40 (43)	33.5 (36)	1.19	35.2 (38)
intercostal	90.2 (100)	29.5 (33)	31 (34)	0.98	35.2 (39)

Coiling is moderately evolute, the umbilicus comprising 38% of the diameter, broad and rather shallow. The umbilical wall slopes gently outwards and the whorl section is a compressed oval (whorl breadth to height ratio is 0.98) with flattened flanks. The phragmocone bears three long, straight, prorsiradiate distant ribs. These arise from small umbilical bullae and also bear conical inner and clavate outer ventrolateral tubercles; there is a siphonal row of distant clavi corresponding in position to the ventrolateral tubercles. Two shorter, intercalated ribs are also present, bearing outer ventrolateral and siphonal clavi only. This same style of ventral ornament is shown on the penultimate whorl, preserved in the dorsum of the body chamber, and in two of the paratypes (Warren 1930, pl. 3, figs. 2-3).

On the body chamber the umbilical bullae decline and the ribs become high, distant, and flared into a ventrolateral horn which supports the outer ventrolateral clavus. There is a poorly defined siphonal ridge, accentuated into siphonal clavi, and the upper ventrolateral and siphonal clavi are linked by broad transverse ribs which show incipient doubling with a riblet developing at both front and rear.

The suture is simple and little incised, with broad bifid saddles.

Discussion. Small size and even ventral tuberculation are the features by which Warren's species is most easily distinguished from *C. woollgari*; other differences are noted on p. 572. There are no other species with which it is likely to be confused. Of interest, however, is the striking resemblance of the holotype to specimens of *C. woollgari* from the Black Hills area of the U.S. Western Interior, which also show a very even and equal number of upper ventrolateral and siphonal clavi, never, apparently developing the intercalated ribs and tubercles of what we take as typical *woollgari*. These specimens (so far as we have seen) are much larger when adult and have horns with a triangular outline in ventral view rather than flares. These Interior examples are obviously close relatives of the Canadian form, although their precise relative ages are not known.

Occurrence. As for types.

Genus LECOINTRICERAS gen. nov.

Type species. *Ammonites fleuriausianus* d'Orbigny, 1841, p. 350.

Diagnosis. Medium-sized, involute during early and middle growth, becoming evolute at maturity. Whorls trapezoidal when young, with sparse conical umbilical tubercles giving rise to pairs of low broad ribs, with occasional intercalatories. All ribs bear outer ventrolateral and siphonal clavi on a fastigiate venter, but the appearance and persistence of inner ventrolateral tubercles is variable. In middle growth the venter often broadens and flattens, the ventrolateral tubercles fuse into a blunt horn and there is a low continuous undulant siphonal ridge, strengthened between horns. The last part of the adult body chamber is contracted, tubular and unornamented except for growth lines, and the aperture is simple.

The suture is simple with broad, asymmetrically bifid E/L, narrower L and smaller bifid L/U₂.

Discussion. The whorl section, massive umbilical tubercles and sparse low ribs of early middle growth, the blunt horns and the tubular body chamber distinguish *Lecointricer* from all other collignoniceratids and the persistence of short ribs on the sides from contemporaneous *Collignonicer*. Some *C. woollgari* develop a short, smooth terminal portion to the body chamber but their

EXPLANATION OF PLATE 73

Figs. 1-4. *Collignonicer* *canthus* (Sornay). The holotype, SP 6793, from Bourré (Loir-et-Cher). 3 is the external mould of the nucleus; 4 shows the decline in ornament over the last part of the body chamber.



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compressed, finely ribbed inner and middle growth stages, much narrower flank ribs, retention of multiple siphonal ribs and clavi is distinctive. This ventral ribbing and retention of clavi also distinguish *C. canthus* and *C. papale*; *C. turoniense* has a smooth body chamber, but lacks the massive umbilical tubercles and ventral horns in middle growth and on the first part of the body chamber. The phragmocone of some *Lecointricer* and the adult shell of *C. boreale* are superficially similar, but Warren's species has compressed finely ribbed inner whorls and on the outer whorl, which is slender and rounded intercostally, the ribs lack a massive bulla, are narrower and produced into a narrow flared bituberculate horn rather than the single broad protuberance seen in *Lecointricer*.

As is discussed below, *Ammonites vielbancii* d'Orbigny, 1850 is a synonym of *A. fleuriausianus*. Schlüter (1871, pp. 21–22) believed the former might be a synonym of *Mammites nodosoides* (Schlüter), and Collignon (1939) and Wiedmann (1960, 1964) referred it to *Mammites*. As Pervinquier (1907, p. 311) noted, the siphonal tubercles are quite distinctive.

In Europe *Lecointricer* first appears in the mid-Turonian St. Cyr-en-Bourg Fossil Bed, accompanying typical *Collignonicer*. Its origins may lie in one of the undescribed *Thomelites*-like forms occurring in the earliest English Turonian.

Occurrence. Widespread in the French Turonian (Touraine and Aquitaine); also occurring in northern Spain, Czechoslovakia, north Germany and southern England.

Lecointricer *fleuriausianus* (d'Orbigny)

Plate 74, figs. 1–10; Plate 75, figs. 1–5; text-figs. 8, 9

- 1841 *Ammonites Fleuriausianus* d'Orbigny, p. 350, pl. 107, figs. 1–3.
- 1841 *Ammonites Woolgari* d'Orbigny, p. 352 (*pars*), pl. 108, figs. 1–3.
- 1850 *Ammonites Vielbancii* d'Orbigny, p. 189.
- 1860 *Ammonites Fleuriausianus* (d'Orbigny); Courtiller, p. 250, pl. 3, fig. 1.
- 1867 *Ammonites Fleuriausianus* d'Orbigny; Courtiller, p. 7, pl. 7, figs. 1–4.
- non 1869 *Ammonites Fleuriausianus* d'Orbigny; Schloenbach, p. 291.
- 1871 *Ammonites Vielbancii* d'Orbigny; Schlüter, p. 19 et seq.
- ?1872 *Ammonites Fleuriausianus* d'Orbigny; Schlüter, p. 28, pl. 10, figs. 1–3.
- 1887 *Acanthoceras Fleuriausianum* d'Orbigny; Laube and Bruder, p. 234.
- non 1902 *Acanthoceras Fleuriausianum* d'Orbigny; Petrascheck, p. 147, pl. 11, figs. 1a–b, 2.
- 1907 *Ammonites Vielbancii* d'Orbigny; Pervinquier, p. 311.
- 1939 *Mammites Vielbancii* d'Orbigny; Collignon, p. 81, pl. 11, figs. 1, 2.
- 1946 *Ammonites vielbancii* d'Orbigny; Sornay, p. 213.
- 1946 *Ammonites fleuriausianus* d'Orbigny; Sornay, p. 214.
- 1960 *Mammites vielbancii* (d'Orbigny); Wiedmann, p. 721.
- 1977 *Collignonicer* (*Selwynoceras*) *fleuriausianum* (d'Orbigny); Hancock, Kennedy and Wright, p. 156.

Type series. *Ammonites fleuriausianus* has been a poorly understood species, although the type figure (if taken to be natural size) is an accurate representation of the middle growth stages and the type series survives. In his original description d'Orbigny recorded the species 'en place dans la craie chloritée ou craie tufau des Martrous,

EXPLANATION OF PLATE 74

Figs. 1–10. *Lecointricer* *fleuriausianum* (d'Orbigny). 1–2, the lectotype of *Mammites vielbancii* (d'Orbigny), MNHP 6779, (d'Orbigny Collection) from Saumur (Maine-et-Loire). 3–5, CS 629b, from the environs of Saumur (Maine-et-Loire), a juvenile of moderate inflation. 6–7, the lectotype, MNHP 6777b (d'Orbigny Collection) from the Calcaire à Céphalopodes of Rochefort (Charente-Maritime). 8–10, FSM 125, from Poncé, Sarthe, a hypernodose juvenile.



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près de Rochefort (Charente-Inférieure); M. Dufrenoy l'a aussi du même lieu; M. d'Archiac l'a observée à Gourdon (Lot); MM. Dufrenoy et Graves l'ont trouvée, aux environs de Saumur' (d'Orbigny 1841, p. 352). In the posthumous catalogue of his collection (dating from 1858-60) the following are recorded:

6777 Saumur, Maine-et-Loire, 3 specimens (4 are present).

6777a Martrous, 1 specimen (missing).

6777b Rochefort, Charente-Inférieure, 2 specimens (3 are present).

6777c Chatellerault, Vienne, 2 specimens (1 missing).

The Saumur specimens belong to at least two species. The first, 34.5 mm in diameter, is a crushed tuffeau specimen, and is labelled [La] Flèche. It has rather flattened flanks, with umbilical bullae giving rise to 2-3 flexuous ribs with some intercalatories, giving a total of sixteen ribs per whorl. There are distinct conical inner ventrolateral tubercles and subequal outer ventrolateral and siphonal clavi, which show it to be a *fleuriausianum*, as is a second individual with an estimated diameter of 55 mm, but having little indication of inner ventrolateral tubercles and weak siphonal clavi.

A third specimen, 71 mm in diameter, and labelled Saumur, is a worn, wholly septate *Jeanrogericeras reveliereanus*. The final specimen has 'Rochefort' written on it in pencil and is also a *J. reveliereanus*, with a diameter of 104 mm. Superficially it could be the basis of d'Orbigny's side view but it lacks all signs of a siphonal clavus.

Two specimens from Rochefort are associated with a plaque labelled 6777b. Both are well preserved on one side, the larger 55 mm in diameter, the smaller 35 mm, and appear to be part of d'Orbigny's original suite. The larger of these, the most typical in the series, is here designated lectotype.

The single specimen to survive of those originally labelled 6777c is a very battered, crushed, distorted specimen in yellow tuffeau. Umbilical bullae give rise to pairs of ribs, terminating in rounded ventral clavi, with no sign of siphonal nodes, suggesting it to be a mammitid or *Jeanrogericeras*. Chatellerault was not mentioned as a locality by d'Orbigny in his original description and thus this specimen is not a syntype.

The types of *A. vielbancii*, herein regarded as a synonym, also present a confused situation. It is a *Prodrome* species introduced (d'Orbigny 1850, p. 189, no. 11) as follows: '*Vielbancii*, d'Orb., Paléont., 1, p. 352, pl. 108, figs. 1-3. Sous le faux nom de *Woolgarii*, Mantell. Martrous, Saumur, Tourtenay.'

In *Paléontologie Française* (1841, p. 354) he cites the species as occurring more widely, but we take these references (which include England) to be to the true *Collignoniceras woolgarii*.

The d'Orbigny catalogue lists the following:

6779 Saumur, Maine-et-Loire, 3 (4 specimens).

6779a Bords de la Vienne, 2 (1 missing).

6770b Rochefort, (illegible) (missing).

whilst d'Orbigny notes that his lateral view (pl. 108, fig. 1) is of a specimen in his collection and the apertural view is of a specimen in the École des Mines.

Inspection shows that the d'Orbigny specimens have become mixed. The Rochefort specimen is present, but labelled 6779. It is poorly preserved, but may be the basis of d'Orbigny's side view. The specimen from the Bords de la Vienne is not a syntype; it is a large *Mammites nodosoides*. As Sornay has discussed (1946, p. 214), the specimen figured in side view by d'Orbigny does not look like any of the poor specimens which survive in his collections under the name *vielbancii*, and certainly there is little resemblance between d'Orbigny's figures and the specimen re-figured by Collignon as 'type'—which we take to be a valid lectotype designation. Even the specimen in the School of Mines upon which d'Orbigny (1841, p. 354) said his apertural view is based (no. A35.3, locality unknown: 'Bassin de la Loire, achète de Stur' reads the label) does not correspond to the figure (compare text-figs. 8 A-C and 9 A-B). We would suggest, in fact, that the illustrations are composite, the side view being based on the poor Rochefort specimen of appropriate size, combined with the ornament of the huge *Mammites* no. 6779a from the 'Bords de la Vienne', the apertural view being based on the School of Mines specimen plus the *Mammites*.

Description. The smallest individuals we have seen are approximately 30 mm in diameter. At this size the coiling is fairly involute (umbilicus = 25% or less of diameter) and the umbilicus quite deep, with a rounded wall. The

EXPLANATION OF PLATE 75

Figs. 1-5. *Lecointraceras fleuriausianum* (d'Orbigny). 1-3, FSM 120, 4-5, FSM 121, compressed and inflated middle-aged individuals from the Turonian of Sarthe.



1



2



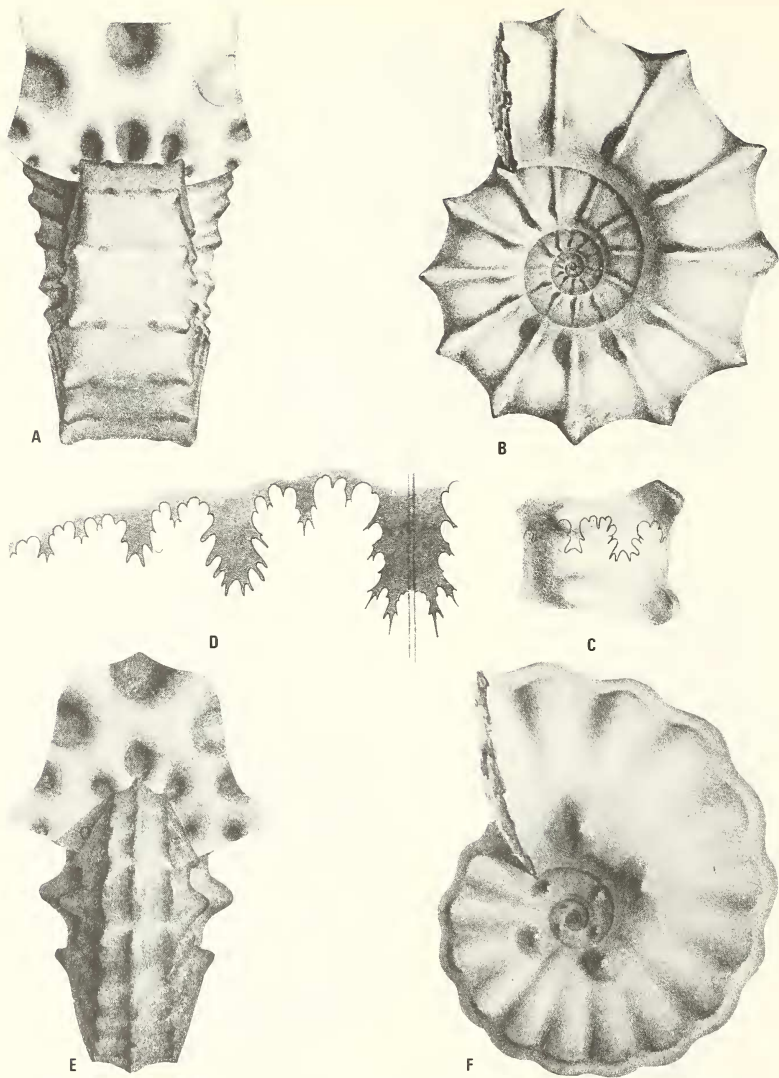
3



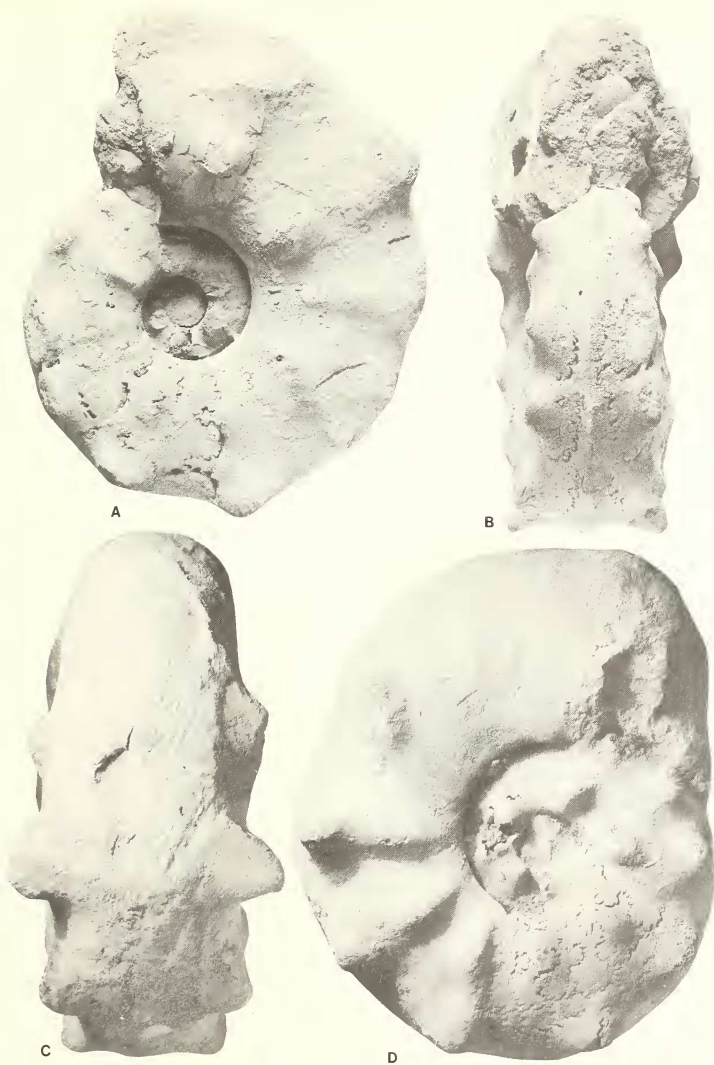
4



5



TEXT-FIG. 8. A-C, copies of d'Orbigny's original figures of '*Ammonites Woollgari* Mantell' (1841, pl. 108, figs. 1-3) = *Ammonites vielbancii* d'Orbigny, 1850. The illustration is said in the text to be reduced by a third and on the plate by a half. D-F, copies of d'Orbigny's original figures of *Ammonites fleuriausianus* (1841, pl. 107, figs. 1-3). The illustration is said to be reduced by a third.



TEXT-FIG. 9. *Lecointriceras fleuriausianum* (d'Orbigny) A, B. EMP A35.3, 'Bassin de la Loire, achète de Stur'—the original of d'Orbigny's (1841) pl. 108, fig. 2. Reduced $\times 0.66$. C, D. FSM 119, an adult from Poncé, Sarthe(?) showing the smooth, tubular termination to the body chamber. Reduced $\times 0.6$ approx.

intercostal whorl section is typically compressed, with the greatest breadth low on the convergent flank and with rounded shoulders and venter. In the costal section the greatest breadth is at the umbilical bulla and whorl breadth to height ratios vary greatly up to 1:2, with concave inner flanks and a fastigate venter.

Ornament consists of weak to strong conical umbilical bullae, 7-9 per whorl, giving rise to pairs of low, broad straight ribs, with occasional intercalated ribs arising low on the flank. The ribs decline somewhat in strength on the mid-flank but then strengthen into rounded inner ventrolateral tubercles. These are connected by a strengthened rib to strong clavate outer ventral tubercles, from which a broad subdued rib sweeps forwards to a subequal clavate siphonal tubercle.

This general style of ornament varies from individual to individual, with slender, feebly bullate forms with weak ribs (Pl. 74, figs. 6-7) and strongly bullate inflated forms with strong ribs (Pl. 74, figs. 8-10). In many individuals, including the lectotype, there are no inner ventrolateral tubercles below diameters of 35-42 mm; occasionally they do not appear until 55 mm.

From 50 mm onwards there is usually a change in ornament; the bullate umbilical tubercles become more distant, the associated ribs lower and broader, effaced at mid-flank in some specimens. There are usually 7-9 bullae and 16-22 ribs per whorl. The outer ventral tubercles weaken rapidly and disappear; at the same stage the inner ventrolateral tubercles strengthen without joining the weakening ventral tubercles (Pl. 77, fig. 4). The former inner ventrolateral tubercles gradually develop into strong to massive horns on the shoulder, triangular when viewed ventrally and relatively narrow when viewed laterally, developed both upwards and outwards. At this, the '*vielbancii*' stage, the venter becomes relatively broad, with a continuous low undulant siphonal ridge, strengthened between horns at what corresponds to the site of the now coalesced siphonal clavi. The shell now closely resembles a *Mammites* in all but the siphonal ridge.

This style of ornament extends onto the first half of the adult body chamber, by which stage the siphonal ridge may become very reduced (text-fig. 9 C-D). On the last half of the body-chamber, extending for just over a quarter whorl, all ribs and tubercles are lost and there is a relatively smooth, compressed and constricted terminal portion with convergent sides, broadly rounded shoulders and a flattened venter, ornamented only by low, prorsiradiate growth striae. The aperture is simple and entire.

The suture line is relatively simple, with a broad medial element to E; broad, asymmetrically bifid E/L; narrow, symmetrically bifid L; smaller asymmetrically bifid L/U₂; and small and narrow U₂.

Discussion. D'Orbigny's original figure is idealized and bears little relationship to the surviving syntypes in his collection; in his explanation of the plate he says the figure is reduced by a third, so that the specimen is far larger than the proposed lectotype, being, presumably, the Martrous specimen which is now lost. The lectotype agrees well with the dimensions given by d'Orbigny for his smaller specimen (1841, p. 350). Juveniles of this species vary in the strength of the umbilical tubercles; the lectotype is worn but was probably a slender, weakly tuberculate variant. This variation continues into middle growth, where both slender and robust individuals are known (Pl. 74, figs. 3-10).

The striking contracted tubular termination of the body-chamber of adults of this species occurs at disparate sizes. Most specimens we have seen appear to be juveniles of individuals that would have been adult at approaching 150 mm diameter, but a specimen in the collections at Le Mans is complete at only 100 mm, with half a whorl of the body chamber so modified. Unfortunately our sample of adults is too small to show if the species shows a size dimorphism.

Some of the early references to this species are doubtful. Schloenbach's (1869) material probably belongs to *Barroisiceras*, whilst Schlüter's specimen (1872, p. 28; pl. 10, figs. 1-3), if indeed a true *L. fleuriausianum*, has suffered great *post-mortem* crushing to give a very compressed whorl section.

Lecointriceris carinatum sp. nov., described below, differs from *L. fleuriausianum* in its smaller adult size, early loss of umbilical tubercles and ribs, together with retention of a fastigate venter on the adult body chamber, which bears an undulose siphonal and flanking, semi-continuous lateral

EXPLANATION OF PLATE 76

Figs. 1-2. *Collignoniceras carolinum* (d'Orbigny), MNHP W8, an adult body-chamber from an unknown locality in the Tuffeau Blanc de Touraine.

Figs. 3-5. *Lecointriceris carinatum* sp. nov. The holotype, EMP, Poncé(?), Sarthe.



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keels formed by coalescence of ventral and siphonal clavi. Differences from *L. costatum* sp. nov. are discussed below.

The combined features of *L. fleuriausianum* as here described are so distinctive that confusion with any other collignoniceratid is unlikely. Juveniles have a passing similarity to some Barroisiceratinae; species of *Barroisiceras* have less prominent umbilical tubercles and many strong, narrow ribs at a comparable size; whilst *Forresteria* and similar genera have an additional, lateral row of tubercles. In middle growth there is a superficial resemblance to *Mammites*, but that genus never develops a siphonal tubercle.

Occurrence. This species is common at the level of the mid-Turonian St. Cyr-en-Bourg Fossil Bed in the Saumur area in Touraine, occurs in northern Aquitaine, Vaucluse, Provence, northern Spain, north Germany(?), and Devon, England.

Lecointricerias carinatum sp. nov.

Plate 76, figs. 3–5

Holotype. A body-chamber in the Collections of the School of Mines, Paris, labelled Poncé(?) and in pencil “‘*Choffaticeras*’ type; ‘*Thomasites*’”. It is clearly from either Poncé or Bourré.

Description. The holotype and only known specimen is a half whorl, largely body-chamber and in typical rather coarse tuffeau preservation. Coiling is very involute with a tiny umbilicus (10% of diameter). The dorsum of the specimen (Pl. 76, figs. 3–5) shows the whorl section of the inner whorls to have been slightly depressed, with the greatest breadth at the umbilical shoulder, concave, convergent flanks and a fastigiate venter. There were sparse umbilical bullae giving rise to low, broad ribs which terminate at elongate ventrolateral clavi, with a sharp siphonal keel, accentuated into clavi which correspond to the ventrolaterals.

On the first part of the body chamber ornament is similar. There are low broad flank ribs which terminate in long clavi linked into undulant keels, flanking a similarly undulant keel in which clavi merge towards the aperture.

The poorly preserved suture shows a typical broad bifid E/L, narrow L, and broad L/U₂, all with only minor incisions.

Discussion. The single known individual is so distinctive that erection of a new species is justified. The inner whorls are typical of a *Lecointricerias*, differing from *L. fleuriausianum* in the sparse, low, broad ribs and presence of keels. Absence of a quadrate-whorled *viellancii* stage makes the body chamber equally distinctive. There is a striking similarity to *Masiaposites* Collignon, 1965, a late Turonian form best known from Madagascar and currently regarded as a vascoceratid; however its siphonal keel is entire and its sutures are much more deeply incised, rather like that of *Neoptychites*, and the siphonal keel continuous throughout ontogeny.

Occurrence. The species is known only from the type occurrence at Poncé(?), Sarthe (mid-Turonian).

Lecointricerias costatum sp. nov.

Plate 77, figs. 1–3

1902 *Acanthoceras fleuriausianum* d'Orbigny; Petrascheck, p. 147, pl. 11, figs. 1–2.

Holotype. AM 55 from the Tuffeau Blanc of Saumoussay, Maine-et-Loire, France.

Other specimens studied. AM 22 from Montsoreau, Maine-et-Loire; AM 53, 54, 60, 101, and 102 from Saumoussay, Maine-et-Loire, France.

EXPLANATION OF PLATE 77

Figs. 1–3. *Lecointricerias costatum* sp. nov. 1–2, the holotype, AM 55, from Saumoussay, Maine-et-Loire; 3, AM 53 from Saumoussay, Maine-et-Loire.

Fig. 4. *Lecointricerias fleuriausianum* (d'Orbigny). AM 36 from Saumoussay, Maine-et-Loire; oblique view to show the concurrent weakening of the outer and the strengthening of the inner ventrolateral clavi.



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Dimensions

	D	Wb	Wh	Wb:Wh	U	R
AM 55 (Holotype)	125.5 (100)	— (—)	53 +		33	c. 21
AM 53	95 (100)	c. 36 ()	c. 44.5	0.81		
AM 60	183 (100)	71	54	0.76		
AM 101	165 (100)					14
	at 129 (100)	50.5	56	0.90	35	17
AM 102	109 (100)	40	45	0.89	30	

Description. This is a moderately evolute and relatively compressed *Lecointricer*, with the greatest whorl-breadth still at the umbilical tubercles in costal section. Of the fourteen to twenty-one ribs slightly less than half are long; the shorter ribs start about halfway up the sides. Each long rib bears an umbilical bulla, a clavus high on the sides rather than in the normal position of an inner ventrolateral, an outer ventrolateral clavus and a siphonal clavus. The siphonal clavi are elevated above the shoulder clavi and up to a diameter of 125 mm may form a nodose keel. During the earlier ontogeny the high lateral clavi are weaker than those on the shoulders, but at diameters which may be anything from 70–110 mm the upper lateral clavi strengthen and the shoulder clavi weaken; the upper lateral clavi eventually become ventrolateral horns on the body-chamber. Similarly the umbilical bullae become weak and are not present on all long ribs beyond diameters of 100 mm. The adult body-chamber begins at about 125 mm diameter, but none of the specimens seen has well-preserved sutures.

Discussion. *L. costatum* differs from *L. fleuriausianum* in having a more compressed whorl section with flatter sides, weaker umbilical tubercles (which are, however, still stronger than in typical *Collignonicer* spp.), siphonal clavi elevated above the outer ventrolateral clavi and persistent outer ventrolateral and upper lateral clavi through much of ontogeny, certainly from a diameter of 40 mm to about 125 mm.

Occurrence. All known French specimens are from the mid-Turonian Tuffeau Blanc of the Saumur region. In that formation ammonites are most common in the St. Cyr-en-Bourg Fossil Bed, but we have not found any specimens of *L. costatum* ourselves; as Amedeo and Badillet (1978) have pointed out, ammonites do occur at other levels in the Tuffeau Blanc. The specimens figured by Petrascheck were from Labiatus-Pläner at Leubnitz and Briessnitz near Dresden in the German Democratic Republic.

EVOLUTIONARY AND STRATIGRAPHIC CONCLUSIONS

The origins of *Collignonicer* and the Collignoniceratidae seem to lie in late *Thomelites* of Acanthoceratidae, the transition involving a raising of the mid-venter and forwards displacement of siphonal clavi and ribs to give a ventral chevron ornament. This is indicated by a few scraps we have seen from the Cenomanian–Turonian boundary beds in Devon. *Lecointricer* may also arise in this way, or be a slightly later offshoot from already distinct *Collignonicer*; the low Turonian record is too poor to be certain. In the United States *C. woollgari* overlaps late *Mammites nodosoides* (W. A. Cobban, *in litt.*); in Europe *C. woollgari* and *L. fleuriausianum* co-occur in the earliest of the French Tuffeau faunas. *C. woollgari* is a long-ranging species which occurs throughout the mid-Turonian zone of which it is the index species. In Europe we have detected no evolutionary changes in the successive *Collignonicer* faunas studied. In contrast, W. A. Cobban's work on western interior sequences allows recognition of an early form, in which both long and short ribs persist in middle and later growth, and a late form in which long ribs dominate. That this is not seen in Europe suggests that typical individuals had reached the U.S. Western Interior by the beginning of *woollgari* Zone time, and underwent subsequent local differentiation which did not occur in European populations. The other collignoniceratids described here are mostly long ranging: *C. carolinum*, *C. papale* and *L. fleuriausianum* range through most of the *woollgari* Zone. *L. costatum* is restricted to the lower part, *L. carinatum*, *C. turoniense* and *C. canthus* to middle and low upper levels in the Zone.

These disappointingly meagre stratigraphic conclusions mean that any subdivision of the broad *woollgari* Zone must be based on other groups. We have already suggested that a local sequence of *Romanicer* can be used in Touraine: *R. (R.) kallesi* (oldest) → *R. (Yubaricer)* *ornatissimum* → *R. (R.) deverianum* (youngest) (Hancock, Kennedy and Wright 1977; Kennedy, Wright and

Hancock, this volume). The lower two of these are clearly correlated with the *woollgari* Zone, but we are not entirely certain whether *R. deverianum* marks a level at the very top of the *woollgari* Zone or at the base of the succeeding *Subprionocyclus neptuni* Zone. Ammonites are too scarce at this level in both England and northern France for us to be sure either way; *Romaniceras* appears to be absent from the rich *neptuni* Zone fauna of the Chalk Rock (Wright 1979) but occurs in the Uchaux (Vaucluse) faunas.

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